

THE ECOLOGY AND MANAGEMENT OF WETLANDS

Volume 1:
Ecology of Wetlands

Edited by
D. D. Hook
and
Others

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This two-volume work presents selected papers from a symposium on wetlands organised by the International Society of Anaerobiosis, held in June 1986 in Charleston, South Carolina. Contributors are international authorities from all over the world, but principally the USA and Europe.

Volume one covers the general ecology of wetlands. Principal subject areas addressed include how plants are adapted to waterlogged soils, plant-animal interactions, soils and geology of wetlands, hydrology and estuarine ecosystems. Volume two covers more applied topics such as agricultural use, restoration and regulation, use for forestry, fisheries and wildlife, the development of wetlands for agriculture and evaluation methods. The volumes represent a definitive statement of the current subject and almost everyone that works with wetlands will find topics of interest in each volume. More specifically, ecologists, botanists and soil scientists as well as workers in forestry, fisheries and wildlife management will find much of value in these volumes.

Edited by Donal D. Hook, Clemson University, South Carolina, and others

THE ECOLOGY AND MANAGEMENT OF WETLANDS

**Volume 1:
Ecology of Wetlands**

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PREFACE

This book contains the proceedings of a symposium held at the College of Charleston, Charleston, South Carolina, USA, 16-20 June 1986. The seed for this symposium arose from a group of physiologists, soil scientists and biochemists that met in Leningrad, USSR in July 1975 at the 12th Botanical Conference in a Session organized by Professor B.B. Vartepetian. This group and others later conspired to contribute to a book entitled Plant Life in Anaerobic Environments (eds. D.D. Hook and R.M.M. Crawford, Ann Arbor Science, 1978). Several contributors to the book suggested in 1983 that a broad-scoped symposium on wetlands would be useful (a) in facilitating communication among the diverse research groups involved in wetlands research (b) in bringing researchers and managers together and (c) in presenting a comprehensive and balanced coverage on the status of ecology and management of wetlands from a global perspective.

With this encouragement, the senior editor organized a Planning Committee that encompassed expertise from many disciplines of wetland scientists and managers. This Committee, with input from their colleagues around the world, organized a symposium that addressed almost every aspect of wetland ecology and management.

The proceedings have been slightly reorganized into a two-volume book that focuses on: (1) the resource and the basic biology and ecology of wetland plants, animals, soils, hydrology and their values and interactions, (Volume I) and (2) the practicality of applying such information to protect and manage the finite wetland resources (Volume II). Within each volume the subject matter has been organized into subject area sections to aid the user to find quickly topics that are relevant to their area of interest.

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Royalties from the book, Plant Life in Anaerobic Environments, were utilized to fund the early organization phases of the symposium, hence, the contributors to the book are commended for helping to perpetuate interest in the wetland resources. The remainder of the symposium costs were funded by registration fees and contributions from the sponsors listed below. We are deeply pleased that support for this symposium came from a broad spectrum of agencies, industries, organizations and universities that reflect the cooperative effort it took to complete this endeavor.

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PART I
THE RESOURCE

Chapter One

GLOBAL WETLANDS - HISTORY, CURRENT STATUS AND FUTURE

Edward Maltby

INTRODUCTION

Wetlands occupy an estimated 6 per cent of the world's land surface. Detailed inventories of types and location, however, are substantially incomplete and information on functions, values and status is extremely limited at the global scale.

Tropical wetlands, in particular are on the whole poorly understood and yet collectively they represent some of the most important areas of the world's remaining wetlands. Optimum utilization strategies for the wide range of global wetlands - including such diverse systems as fresh, brackish and saltwater marshes, inland and coastal swamps, floodplains, mires (all peatland types) and shallow water bodies - are generally at the earliest stages of research and development. Yet the coupling of sound management policy to the scientific understanding of how wetlands work and what goods they provide and services they perform is essential if rapidly diminishing ecosystems are to be maintained for the future.

A global view of wetland resources is most timely and particularly appropriate in the context of this conference. There are stark contrasts between the developed and developing worlds in terms of the ecology and management priorities of their wetland resources. It is imperative to recognize this distinction in any assessment of the current demands on the scientific community.

THE RESOURCE

Wetlands vary according to their origin, geographical location, water regime, chemistry, dominant plants and soil or sediment characteristics. Marshes are dominated by herbaceous plants and sustained by water sources other than direct rainfall. They include some of the most productive ecosystems in the world. Tidal salt-marshes are typical of temperate shorelines and dominate large areas of the eastern seaboard of North America and coastal Europe. Freshwater marshes, dominated by grasses and sedges, account for over 90 per cent of the wetland area in the United States (excluding Alaska and Hawaii) but occur in all latitudes where ground-water, surface springs or streams cause frequent flooding. One of the world's largest marshes is in the Florida

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Everglades, once covering over 1,000,000 ha from Lake Okeechobee to the southwest tip of Florida. The summer flooding pattern of the undeveloped remnants, now substantially protected within the 500,000 ha of the Everglades National Park, is no longer natural.

Swamps are flooded throughout most or all of the growing season and develop in still-water areas, around lake margins and in parts of floodplains. Varied terminology means that they include both forested systems such as the Cypress swamps of the Southern United States, the Melaleuca swamp forests of New Guinea or the mangrove forests of the tropical coasts as well as herbaceous systems such as reedswamps occurring in North America, Europe, Asia, Australasia and South America and also the papyrus swamps which are so characteristic of many African wetlands. The form of many large tropical African lakes - Chad, Bangweulu (Zambia), George (Uganda), Naivasha (Kenya), Malombe (Malawi) and Chilwa, (Malawi/Mozambique) - favors marginal swamp and there may be more swamp than open water in tropical Africa (Beadle, 1974). More than a quarter of Indonesia is swamp, in Sumatra the proportion is 30 per cent. Kalimantan supports nearly 20 million hectares of swamp, more than half with peaty soils.

The world's mangrove forests cover at least 14 million hectares and are concentrated in some of the poorest nations. The greatest concentration is in the Indian Ocean - West Pacific region with about 20 per cent of the world's total area bordering the Sunda Shelf region enclosed by Vietnam, Thailand, Malaysia, Sumatra, Java and Borneo. The Niger delta has 700,000 ha and the Sundarbans forest covers nearly a million hectares of the Ganges delta - where relative remoteness in addition to any intrinsic or special ecological factor has conferred on them special habitat value for the man-eating Royal Bengal Tiger.

Once thought to be restricted almost entirely to high latitudes of the northern hemisphere, peatlands are now considered to cover at least 500 million hectares from tundra to tropical environments. Peat produces distinctive wetland landscapes of bog, moor, fen and muskeg but also forms in association with marsh and swamp in tropical and subtropical lakes, floodplains and coastal regions. More than 75 per cent of all peat soils in the tropics are found in one large concentrated area bordering the western, southern and eastern extremities of the South China Sea. These resources together with those in higher latitudes are attracting increased attention for fuel and other destructive uses. Their role as geochemical and particularly carbon sinks is still imperfectly understood and there is growing concern for global implications of changes in the atmospheric carbon balance associated with their large scale exploitation (Maltby, 1986; Winkler and De Witt, 1985).

The periodic flooding of land between river channels and valley sides is a common feature of the lower reaches of rivers throughout the world and produces a complex variety of wetlands depending on climate, water regime and form of the floodplain. In the United States some periodically flooded areas produce the bottomland hardwood forests. Such forests once covered vast areas of the South East, East and Central United States. The largest contiguous areas occurred in the lower Mississippi River Valley. The bottomland hardwood wetland type still covers more than 23.5

million hectares in the United States. However the wetland complexes once characterizing the fringing floodplains of Europe and North America have now largely disappeared through the deepening of river channels, levee construction and land development. The world's remaining major seasonal floodplains are now limited to the tropics and subtropics but they are under increasing pressure from development projects.

Nearly half the total wetland area of Africa consists of forested or savanna floodplain (Drijver and Marchand, 1985). In special circumstances deltas form and produce a mosaic of wetland types on the African continent. These may be inland such as the Inner Niger and the Okavango or coastal such as the Nile. In some areas the terrain is so flat that seasonal rainfall can produce flooding over large areas. Extensive sheet flooding occurs in the basin of the Chari-Lagone River in Southern Chad. The floodplain grasses can produce 10 t DM ha⁻¹ and the area sustains large populations of wild ungulates and domestic livestock.

Some of the largest sheet flood regions are in South America. The Gran Pantanal of the Paraguay River comprises shallow interconnecting lakes and wetland complexes, which in some years can cover 10,000,000 ha and the Apure-Aranca tributaries of the Orinoco in Venezuela produces a floodplain of 7,000,000 ha.

Man-made wetlands - reservoirs, ponds, lagoons, extraction pits, waterways and, more recently, mimics established as mitigation for wetland losses elsewhere - are an increasing feature of both the developed and developing world. Many are close to concentrations of population which increases their educational, scientific and recreational values. They have become some of the most important wildlife habitats in Western Europe. Such has been the loss of wetlands that 'virtually any water body assumes conservation value' (Tydeman, 1984). Man's ability to create artificial wetlands has led developers to argue against unnecessary protection of natural wetlands where they can be replaced or recreated. The concept of mitigation is an important one in terms of the wetland resource but its acceptability depends inter alia on the ability of artificial wetlands to mimic functions as well as appearance.

WETLANDS IN RETROSPECT

Wetlands have played a key role in sustaining early prehistoric cultures such as the Mesolithic occupants of postglacial lake margins and coasts in Europe. The floodplain environment of the Nile, Tigris and Euphrates was an important factor in the development of major civilizations. There is still a strong dependency on wetland resources by largely subsistence communities in the Third World but the history of wetlands in the developed world has been one of progressive detachment from direct human utilization and conversion to non-wetland uses. There is a certain irony that the current surge of scientific and social interest in wetland ecosystems coincides with the period when many of the world's developed countries already have destroyed or altered the greater part

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of their original wetland area to make way for agriculture, industry, urban and other land uses.

Fifty four per cent of the wetland area of the coterminous United States present in colonial times had been lost by the mid 1970s (Tiner, 1984). Regional losses detailed in the benchmark survey by Tiner (1984) as part of the US Fish and Wildlife's National Wetland Inventory vary from 32 per cent in Wisconsin to 99 per cent in Iowa's natural marshes. The pattern is repeated throughout the developed world, although there has been no comprehensive survey of the details. Forty per cent of the coastal wetlands of Brittany, France, have disappeared in the last 20 years and two-thirds of the remainder are seriously affected by drainage and other activities (Mermet, cited by Baldock, 1984). In Ireland, 80,000 ha of bog have been drained since 1946. A 1983 European parliament report warned that 'the unique ecosystems of the Irish bogs will vanish completely in the next five years unless effective preventative measures are taken very soon' (Baldock, 1984). But already before the present century much of Europe's lowland wetlands had been drained in the course of agricultural development and disease eradication.

Large-scale wetland losses have been a more recent phenomenon in the tropics and Third World countries. However, enormous losses have occurred in a short space of time and only 25 per cent of the original mangrove area of 24,000 ha is left in Puerto Rico and in Southeast Asia conversion of natural mangrove ecosystems into rice paddy and aquaculture has been occurring at an unprecedented rate in recent years (de la Cruz, 1980). Between 1967 and 1975 an annual loss of 24,000 ha was reported from the Philippines. At least 5,000 ha yr⁻¹ are lost in the production of wood chips in Malaysia and Thailand has lost up to 20 per cent of its mangrove cover in the past decade (MacIntosh, 1983).

Why Has Progressive Loss Taken Place?

Many reasons can be cited why, historically, wetland destruction and alteration has dominated over an alternative view of maintaining them and developing management strategies for their enhanced utilization. They include:

- (a) Prevalence of the 'wasteland' concept - the view that drainage and conversion to other uses is a 'public-spirited endeavour' (Baldock, 1984), resulting in increased productivity, value or access to land. Agricultural conversion has accounted for 87 per cent of wetland losses in the United States.
- (b) Association of wetlands with disease particularly malaria and schistosomiasis and physical danger in traversing such areas. This was one of the motives for draining the 6,000 ha Hula papyrus swamp in northern Israel in the 1950s.
- (c) The obvious flooding hazard associated with occupation or use of such land - periodic extreme events exert pressures for protection thereby reducing the natural flooding regions. Progressive drainage of the English Fens was encouraged by public and political response to successive major flood events (Darby, 1983).

- (d) Lack of government interest. Politicians are rarely gripped by the subject of wetlands and they rarely admit to responsibility beyond their own administrative or national boundaries which wetland issues demand. Control over wetlands also exposes in democratic communities tantalizing questions of rural land use, ownership restrictions, state control and inevitable conflicts of interest on the part of government.
- (e) Lack of financial support for wetland protection and management. This is particularly acute in Third World countries.
- (f) Lack until recently of any individual scientific identity or a cohesive form of academic study centered on wetland per se. This has delayed the dissemination of fundamental and management information.

WETLANDS IN PERSPECTIVE

The results of wetland loss historically on environmental, ecological and socio-economic values have not gone unnoticed. Problems such as those resulting from peat shrinkage, oxidation and erosion have been observed worldwide this century in the English Fens, the United States Everglades, Rwanda, Israel and Jamaica. But communication of the values and functions of wetlands has attracted detailed research only within the last decade and despite a growing literature there is still only a very rudimentary level of understanding, especially in the Third World.

In the Third World whole communities depend on wetland resources for survival; cultures and life styles revolve around flooding cycles and the harvesting of wetland products. The swamp sago (Metroxylon sagu), an important component of the floodplain swamps of Southeast Asia, provides the main food staple for a quarter of the population of Irian Jaya and over 100,000 Papuans (Koonlin, 1980). Over 25,000 villagers around Lake Chilwa on the Malawi-Mozambique border rely on the lake-edge fishery. Here, as with lake and floodplain rivers throughout the world, the annual migration and spawning of fish in the marginal wetlands depends entirely on the flood cycle. Its success is vital to the survival of the fishing communities. In the Lower Mekong Basin 236,000 tons out of a total catch of 500,000 tons per year is estimated to be derived from wetlands. In 1981, the fisheries value of wetlands contributed \$90 million to the economy and supplied 50-70 per cent of the protein needs of the delta's 20 million people (Pantulu, 1981). Shrimp exports from poor countries to the rich nations are currently worth \$900 million a year. Apart from fishing, wetlands provide the basis of flood recession agriculture and floating rice cultivation, transhumance herding of domestic livestock and hunting of wild herbivores migrating in response to flooding patterns. Over half a million wild herbivores, mainly antelope, live on the Sudd floodplains along the Nile in Sudan and hunting provides up to 25 per cent of the annual meat intake of the local people (Drijver and Marchand, 1985).

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Wetland Functions and Values

The rational use and management of wetlands requires a thorough knowledge of how they function and interact with the environment and what goods and services they provide for (1) direct and indirect human use; (2) the welfare of wildlife, and (3) environmental maintenance.

Despite the undoubtedly progress in understanding how wetlands work and why it might be important to maintain or enhance them as natural ecological functional units there are a number of problems.

- (a) Current knowledge on functions, values and the development of evaluation procedures is heavily biased towards the developed world.
- (b) Wetlands are extremely diverse, they do not all perform the same functions and values. Similar wetlands may vary considerably according to geographical and socio-economic context.
- (c) The measurement of values generally lacks a common scale. Whilst there are real economic values (such as natural grazing for harvested species or flood protection) which can be attributed to wetlands the basis for calculation of these is often disputed especially where efforts have been made to express them in dollar terms (Larson, 1983) and some qualities have indefinable economic values.
- (d) The driving force maintaining the wetland often originates outside the immediate wetland area and the benefits may be realized elsewhere at some distance, within a different administrative area or another country. What incentive is there for a country to maintain its wetlands, sacrificing other development options, if the benefits are felt outside the country?

WETLANDS IN PROSPECTIVE

Reaction to a range of key issues will determine the future of the world's wetlands and some of the more salient are highlighted.

Information Gaps

These fall into several different categories.

- (a) Fundamental knowledge of location, characteristics, functions, values, threats and assessment.
- (b) Applied data on management strategies for sustained utilization of wetland resources.
- (c) Consequence of alternative development.

International Union of Conservation of Nature and Natural Resources (IUCN) directories of wetlands of international importance have been completed for the Palearctic and Neotropical Realms. Volumes for the Afrotropical and Australasian regions are in preparation. Necessarily they can deal only with those wetlands considered most important and there is still a heavy bias on value

for waterfowl. The need for much more comprehensive coverage of wetlands rests with individual nations but in the case of the Third World this will undoubtedly require assistance from external sources.

A major aim of the current WWF/IUCN Wetlands Conservation Program is to establish at the IUCN Conservation Monitoring Centre (CMC), Cambridge, England, a Wetlands Data Base. The data base will include information on the value of wetlands to society and especially how these values can be maintained while simultaneously attempting to meet the legitimate development needs of human communities. The Centre for Environment Studies, University of Leiden, The Netherlands is currently involved in establishing information compatible with the CMC Data Base on the impacts of various development schemes, the types of wetlands development which maintain ecological processes and the means by which to improve existing project design of schemes such as drainage, polders and dams which pose increasing threats to traditional wetlands throughout the developing world (Project EDWIN).

Project EDWIN focuses on the developing countries of the tropics. It is here that the greatest pressures exist from development projects, from aid agencies and governments but it is here that the greatest gaps in empirical scientific data exist and where the training needs to develop the skills required for sound management policies are at a premium.

Comparisons are required of the productivity of the natural system with that of modified systems such as irrigation agriculture, the losses which occur due to alteration of wetlands and the gains which might be realized by enhanced management of the wetland resources. Detailed balance sheets need to be drawn up which evaluate not only the net sustainable benefit to local communities and the national economy of the ecological and environmental processes performed by wetlands but also the advantages (local, national and international) where they exist over alternative development strategies.

There is an ever-pressing need to provide information on (1) the relationship between wetland area/condition and value of ecological services, e.g. fishery production, and (2) the point where loss or alteration of the wetland regime becomes critical for sustained performance of services or inability for the system to recover after change or impact.

State Support and Subsidies

Governments of the developed world continue to pay for the destruction of wetlands through drainage grants, public funding of major alteration projects, favorable tax structures and artificial price support for crops grown on reclaimed land. European taxpayers pay to have the wetland converted, pay in various ways for the loss of wetland functions and then pay subsidies and storage costs of the surplus produce grown on the former wetland. However, in Britain a recent milestone was achieved in 1985 when the Ministry of Agriculture, Fisheries and Food won European Community approval to aid traditional agricultural practices needed to maintain the wetland environment of the Norfolk Broads rather

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than financing intensification and ecologically damaging drainage (O'Riordan, 1985).

The future of the remaining wetland landscape of the developed world surviving outside areas protected for nature conservation is subject to economic forces and political pressures which are balanced against desirable functions of wetlands. The best hope for maintaining a significant proportion of the existing wetland areas is to inform and continually educate planners, politicians and decision-makers as to their values and functions.

International Dimensions of Wetlands

Wetlands are natural systems; their boundaries rarely follow national frontiers:

- (a) some wetlands cross national boundaries;
- (b) the maintenance of essential wetland systems may depend on water flows or pulses originating externally;
- (c) the benefits or values of wetlands may be realized externally and not necessarily 'on site'.

Lake Chad has been receding fast in recent years (40 km in the Nigerian sector between April 1984 and January 1985) and not simply due to drought. The lake is fed mainly by the Logone and Chari Rivers in Cameroon. Major dams are now diverting water from these rivers to major irrigation projects. Unless the catchment countries - Nigeria, Niger, Chad and Cameroon - can be persuaded of the need to treat the Chad basin as an international resource any direct attempt to manage the wetland complex of Lake Chad will be a futile exercise.

The case of migratory waterfowl emphasizes the internationalism of wetlands and underpins the efforts of international protection embodied within the Ramsar agreement. But there are more clear economic reasons for international cooperation to maintain wetland resources. It has been estimated that as much as 80 per cent of the Indian fishery catch from the lower delta region of the Ganges/Brahmaputra comes from the Sundarbans (Christensen, 1983). Thus recent agreement to increase the dry season flow of freshwater (these areas are frequently interrupted by barrages, irrigation and ground-water abstraction, Maltby, 1986) not only benefits the wet forest and mangrove complex but also helps to maintain much needed fishery resources. The latter benefits both India and Bangladesh. Effective wetland management requires integrated management of the whole catchment on which the wetlands depend.

Role of Foreign Aid and International Development Banks

Most of the engineering and land projects causing removal or disruption of wetlands in the Third World are backed by foreign expertise and funding and frequently by aid packages. Dutch engineering companies have been involved in more than half the 180 large polder projects (areas originally open to 'normal' flooding now impounded and water levels controlled artificially or more

commonly drained completely) carried out or planned in the last 20 years (Braakhekke and Drijver, 1984). In only 5 per cent of cases has any serious study been made of the consequences of reclamation for the nature values and functions of the area affected. Decisions about exploitation or changes of wetlands are generally made in the Third World without detailed reference to local usage or without assessment of the wider benefits of the natural system with or without alternative management strategies. Donor or exporting nations, especially those that are Ramsar signatories, have an obligation to take account of the possible impacts in the first stage of survey and planning; not after actions have been taken.

Special Problems of Poor Countries

The political debate over Third World wetlands is usually expressed as a straight choice of either:

- (a) converting them to specific use, i.e. short-term direct food production, high density aquaculture or intensive livestock rearing (or using them for foreign currency savings through peat mining or other commercial activity) or
- (b) conserving them for long-term economic, ecological and environmental reasons.

'We cannot afford not to develop' is the common argument used not only by politicians but also by environmentalists in poor countries. One of the most recent potential developments in the tropics is the mining of peat for energy. The chance to reduce fuel import bills and balance of payments deficits, establish local industry, reduce fuel wood losses, provide local employment and raise standards of living is understandably tempting to countries like Jamaica, Indonesia, Rwanda and Burundi. The development of new technology for wet extraction of peat, for handling large residual wood content and mechanically dewatering in humid climates exposes the coastal and inland peats of the tropics to increasing threat. In Southeast Asia and Africa plans for exploitation are well ahead of investigations of possible adverse impacts. Only in Jamaica has there been any serious attempt to examine environmental consequences of peat mining.

THE ROLE OF WETLAND SCIENTISTS

The challenges to the scientific community of maintaining the wetlands of the world is quite clear and must be taken up at three related levels (Table 1.1). Some wetlands are rare or uniquely important and require complete protection for nature conservation reasons. However, this is not an effective argument to use in preventing loss or degradation of the remaining wetlands of the world. The future of these areas lies in their sustainable utilization and on demonstration of their values as wetland ecosystems versus competitive land uses. There are still basic research needs in understanding wetland processes and the greatest advances are likely to be made by ensuring that multidisciplinary and inter-

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national teams cooperate. Greater research thrust in Third World wetlands is badly needed particularly in relation to values such as food chain support and water quality. A major aim must be to provide the guidelines necessary which will allow decision makers to assess wetlands fully and rationally. It is clear that more research must be applied, e.g. determining ways of enhancing the natural productivity of wetlands or devising optimum management strategies such as harvesting or utilization of resources. This will be a much more attractive approach to Third World governments, aid agencies and development banks than one based on the more conservation-orientated philosophy on which wetland maintenance in the developed world is often argued.

It is equally important that research findings are translated into training programs. This must include not only basic and advanced educational courses but also the development of specific management programs. Pilot wetland conservation projects have been proposed already by WWF/IUCN in Brazil, Central America, the Sahel, coastal West Africa, Southern Africa, China and Indonesia. These need to be sustained as long-term projects, expanded and used as a springboard for a higher level of scientific involvement with management schemes demonstrating particularly in the Third World the practical utilization of wetland resources.

There is an increasing need for exchange of information and ideas between the scientific community and Non-government Environmental or Conservation Organizations (NGOs) which will

Table 1.1: Role of the scientific community in future wetland research and management

RESEARCH
Multidisciplinary cooperation
Multiagency and international funding
Involvement of governments and development organizations
Problem orientated
Emphasis on sustained utilization
Long term
TRAINING
Education
Management
Task forces
Pilot schemes
INFORMATION TRANSFER
Non-government Organizations (NGOs)
Media
Public
Conferences

ensure that the lobbying of politicians, aid agencies, financial institutions and major development organizations is carried out on a scientifically informed basis. If wetland issues are popularized and the scientific problems explained through the media then the informed general public can become a potent force in developing sound wetland policies for the future.

CONCLUSION

Wetland utilization has been regarded traditionally in what was regarded in another context by Sauer (1938) as a 'passing frontier of nature replaced by a permanently and sufficiently expanding frontier of technology'. This attitude he goes on to say 'has the recklessness of an optimism that has become habitual but which is residual from the brave days when north European free-booters overran the world and put it under tribute. We have not yet learned the difference between yield and loot. We do not like to be economic realists.' That reality could now be realized. It will be achieved when there is more general acceptance of the concept of the World Conservation Strategy, (IUCN, UNEP, 1980), that wetland ecosystems are not inherited from our ancestors but borrowed from our descendants. They must be returned in good working order - if they are returned with interest so much the better.

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Chapter Two

THE FUNCTIONS OF A PRISTINE ESTUARINE ECOSYSTEM*

F. John Vernberg

INTRODUCTION

The science of ecology has made remarkable advances in the past years. Numerous factors have helped nurture and stimulate ecology's exponential growth. Societal awareness of the rapid deterioration of the planet earth's environment has certainly placed a demand upon the ecological community to answer questions and to develop new hypotheses on how organisms, including the human species, interact with their complex abiotic environment. Not only have ecologists become more aware of how a single organism struggles to survive but, very importantly, ecologists are striving to understand how biotic systems involving communities of organisms cope not only in response to 'normal' environmental changes but also in response to man-induced perturbations. This systems approach, although not new to science, has recently focused on the structure and function of the various components of an ecosystem with ever-increasing vigor.

One sector of the earth's landscape which will be highlighted in this paper is the coastal zone including wetlands and estuaries. These habitats are globally distributed and, because of their strategic location, human society has long been associated with them. Not only are they highly productive biologically but they support a wide range of economic activities. Two indicators of their importance are (a) at present, 33 per cent of the United states population lives and works in areas adjacent to estuaries; and (b) on a worldwide basis, seven of the 10 largest metropolitan areas border existing or former estuarine regions (New York, Tokyo, London, Shanghai, Buenos Aires, Osaka and Los Angeles). Depending on the information source, it is predicted that by the year 2000, 70-80 per cent of the world's population will be living in coastal lands (Ketchum, 1972; The Global 2000 Report to the President, 1980; Archer, 1982). This projected growth pattern will lead to rapid rates of coastal settlement and urbanization, especially in lesser developed countries. Obviously these dramatic changes will greatly alter the ecological nature of estuaries and wetlands if

*Contribution number 634 from the Baruch Institute, USC.

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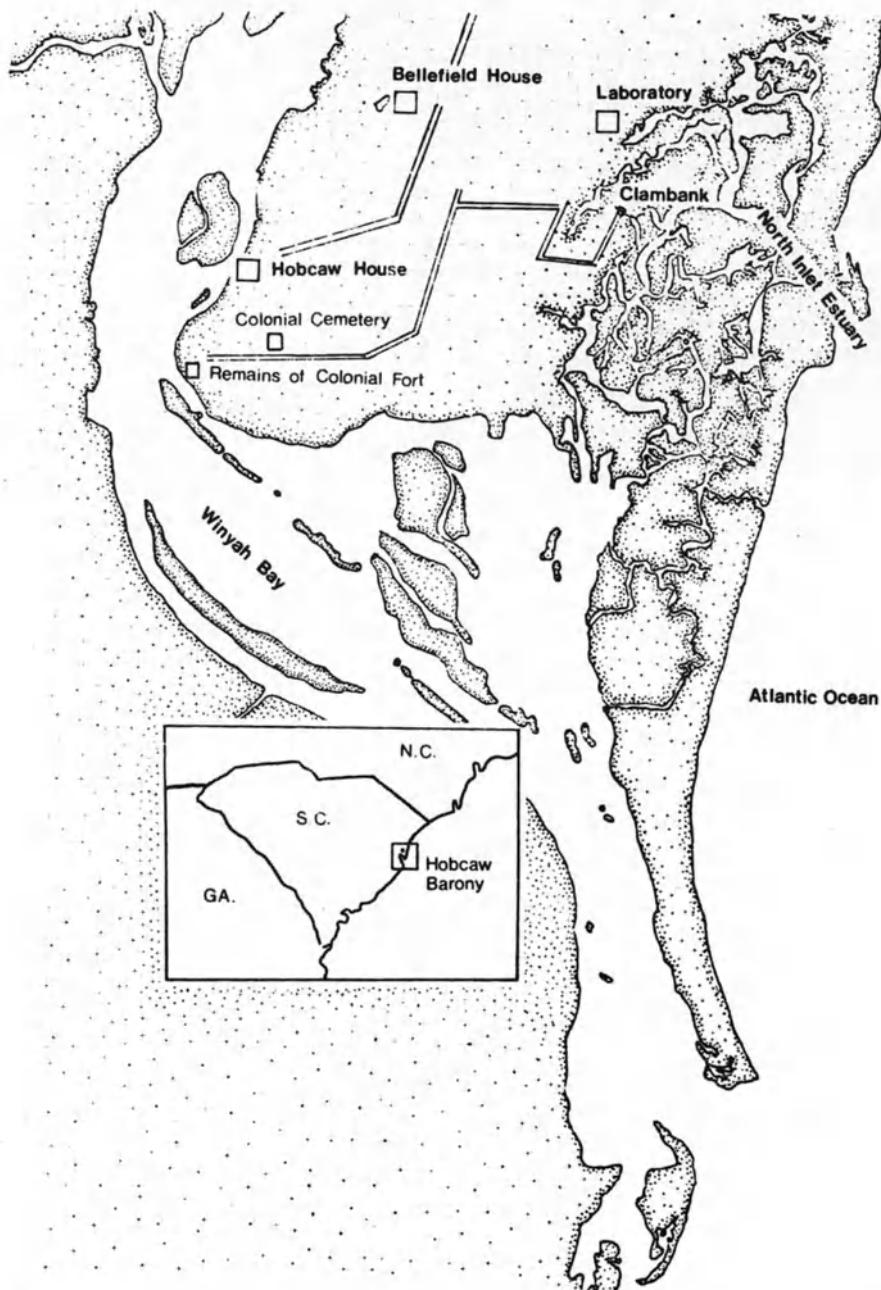
society does not demand more stringent conservation and management practices. Within the framework of these unceasing developmental demands, it is obvious that many of the undisturbed coastal areas will be dramatically altered. This global assault on estuaries and wetlands places the ecologist in the difficult position of trying to develop an understanding of estuarine ecosystem dynamics at a time when the estuaries are constantly being impacted in an unpredictable manner by human activities. Therefore an urgent need exists to study undisturbed, pristine estuarine ecosystems in order to have a basic understanding of how 'normal' ecosystems function. Knowledge of the dynamics of a 'normal' system will provide a standard to which other estuaries in various stages of alteration can be compared. The development of new ecological systems theories is dependent upon understanding how unperturbed systems work in comparison with those undergoing anthropogenic shock. Rather than document the impacts of past destruction of wetlands and the dire consequences of future manipulation, even though this is extremely important, I will emphasize the role of studying extant pristine estuarine-marsh systems with special emphasis on the North Inlet System located near Georgetown, South Carolina.

NORTH INLET ESTUARINE ECOSYSTEM

Estuaries of the southeastern sector of the United States are characterized by a connection to the sea through which sea water surges in and out on a tidal rhythm. The resultant extensive intertidal zone is typically dominated by single species of vascular plant, Spartina alterniflora. As characteristic of estuaries, a source of freshwater dilutes the oceanic sea water thereby reducing the salinity. Although estuaries vary in size, shape, and structure, they have many characteristics in common; for example, tidal dynamics, nutrient rich, salinity variation, and decreasing number of species with decreasing salinity. The North Inlet System has all of these characteristics and is an excellent example of an undisturbed southeastern estuary. It should be noted that the use of the term 'undisturbed' and 'pristine' to describe the North Inlet System does not imply that this area has not been frequented by humans. Relative to most other estuarine systems in the United States, the North Inlet System has been subjected to little man-induced alterations. Most of the highlands surrounding this system are owned by two private foundations (the Belle W. Baruch Foundation and the Tom Yawkey Foundation), who dedicated their lands in perpetuity for the study of forest and marine systems and will not permit upland development.

North Inlet is located 110 km northeast of Charleston, SC and encompasses about 3,000 ha (Figure 2.1). A number of distinctive habitat types exist within the North Inlet Estuary. There are approximately 2,600 ha of marshland, chiefly dominated by Spartina alterniflora. Oyster beds and reefs are extensive; other intertidal zone habitats include open sandy beaches, protected sandy beaches, mud flats having varying admixtures of different-sized sand-mud particles, dunes, marshy and forest habitats.

Figure 2.1: Location of Field Laboratory, Belle W. Baruch Institute for Marine Biology, USC, on Hobcaw Barony, Georgetown, SC



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From a physical as well as a biological point of view the North Inlet Estuary is a dynamic environment. The semi-diurnal tide has a mean range of 1.6 m; however, during spring tides the tidal range has exceeded 2.2 m with associated maximum currents of 1.4 $m\ s^{-1}$. The estuarine waters usually have salinities in the range from 30 to 34‰, due to low freshwater runoff into the system. However, after frontal passages or summer rain-thunder storms, the salinity has been measured as low as 4‰ in the upper reaches of some creeks.

North Inlet is vertically homogeneous, with a weak horizontal salinity/sigma- σ gradient from the inlet to Winyah Bay. The major variation in the above physical parameters is explained by fluctuations due to the tidal wave, thus North Inlet is a tidally dominated estuary. North Inlet is classified as a type 1-a estuary in the Hansen-Rattray system. Many southeastern estuaries apparently fit this type which is an advantage in mathematical modeling of estuaries, as variations with respect to depth may be of minor importance, allowing for the use of vertically integrated hydrodynamic equations in any flow-simulation effort.

For intensive study of short-term and long-term ecological processes, the North Inlet System is ideal for a number of reasons. First, the boundaries of the estuary are well-defined. Secondly the estuary and marsh lands are relatively undisturbed. Its waters are classified as 'highest quality' by the South Carolina Department of Health and Environmental Control. The estuary is sufficiently small to be studied, but large enough to have distinctive estuarine characteristics. The inlet is approximately 900 m wide. The distance from the inlet to the pier at Clambank is approximately 3000 m by boat. Thirdly, the marsh lands and estuary are sufficiently large to permit experimental manipulation and control of experimental areas, and extensive land holdings provide space for construction of experimental ponds. Extensive oyster beds, as well as large populations of other commercially important species, such as blue crab, shrimp and mullet, are found in this region. Fourthly, study of the biota and physical parameters of the marshes and estuary has been in progress since January, 1970. Although far from being a complete study, data from these investigations furnish a realistic basis for future studies. Tide elevation, wind speed and direction, atmospheric pressure, and rainfall have been recorded continuously for more than six years. To make the biotic and abiotic data readily available to investigators, a well-developed data management system exists (for details contact the author). Fifthly, the flow exchange between the estuary and the Atlantic Ocean and Winyah Bay takes place in a few well-defined creeks which have been monitored. It is possible to determine inputs of water and nutrients from groundwater, terrestrial runoff, and rainfall. Sixthly, most of adjacent wooded highlands and the marshes are owned and protected by the Belle W. Baruch Foundation. The University of South Carolina has a long-term contract with the Foundation to manage the marine area. This arrangement insures protection for long-term studies. Seventhly, a staff of 70 associates has demonstrated not only its ability in studying separate problems associated with coastal environments, but also its ability to work on complex problems in a

coordinated interdisciplinary manner. The resident staff presently numbers 25. Eighthly, laboratory, boat and dormitory facilities are adjacent to the estuary, and finally, the North Inlet System is the only marine site to be included as part of the Long-Term Ecological Research Program funded by the National Science Foundation.

ECOLOGICAL MODELING

Various types of ecological models have been developed to gain insight into how the North Inlet coastal ecosystem functions. In Figure 2.2, a general conceptual model of the estuary which consists of a number of subsystem components is represented. Over the past 15 years, detailed studies on various subsystem processes have been completed and the scope of work has been broadened to include the upland forested areas. Hence, studies are now focused on an ecological landscape which extends from the coastal oceanic waters across the estuarine-salt marsh complex to the coastal maritime forests.

One aspect of this model (the exchange of material across the ecosystem boundary) was studied from 1978 to 1982. A persistent question which has relevance both to resource management of marine waters and to basic ecosystem theory is whether or not there is a net loss (outwelling) of biological and non-living materials from estuaries to the ocean and surrounding regions. To help answer this question, a daily and seasonal synoptic sampling program was instituted in the North Inlet Estuary. Water-related parameters measured were freshwater input, tidal exchange, nutrients, detritus, sediments, ichthyoplankton, zooplankton, phytoplankton, and microbial biomass. Additionally, the movement of materials in or out of the estuary by birds was estimated. Based on these examinations certain trends are apparent. Net yearly export occurred for all classes of materials except zooplankton. Seasonal changes in planktonic components were observed. The composition of materials changed with the tidal cycle, such as microbial biomass and phytoplankton, indicating food chain interactions within the estuary. The export of nutrients was greatest on spring tides. Freshwater input to tidal flow was small, most coming from rainfall. These data have been incorporated into a 19-compartment deterministic model developed to simulate carbon/energy exchange.

LONG-TERM ECOLOGICAL RESEARCH

In response to a well-documented need to study ecological phenomena on a long-term basis, the National Science Foundation has established a program on Long-Term Ecological Research (LTER). The National Science Foundation currently funds research at 11 LTER sites throughout the United States, many having an emphasis on wetlands (Figure 2.3). Some of these sites are in their second five-year cycle of funding. Although intersite diversity in research approaches exists, the following common-core research questions

Figure 2.2: Generalized conceptual model of the North Inlet estuarine system

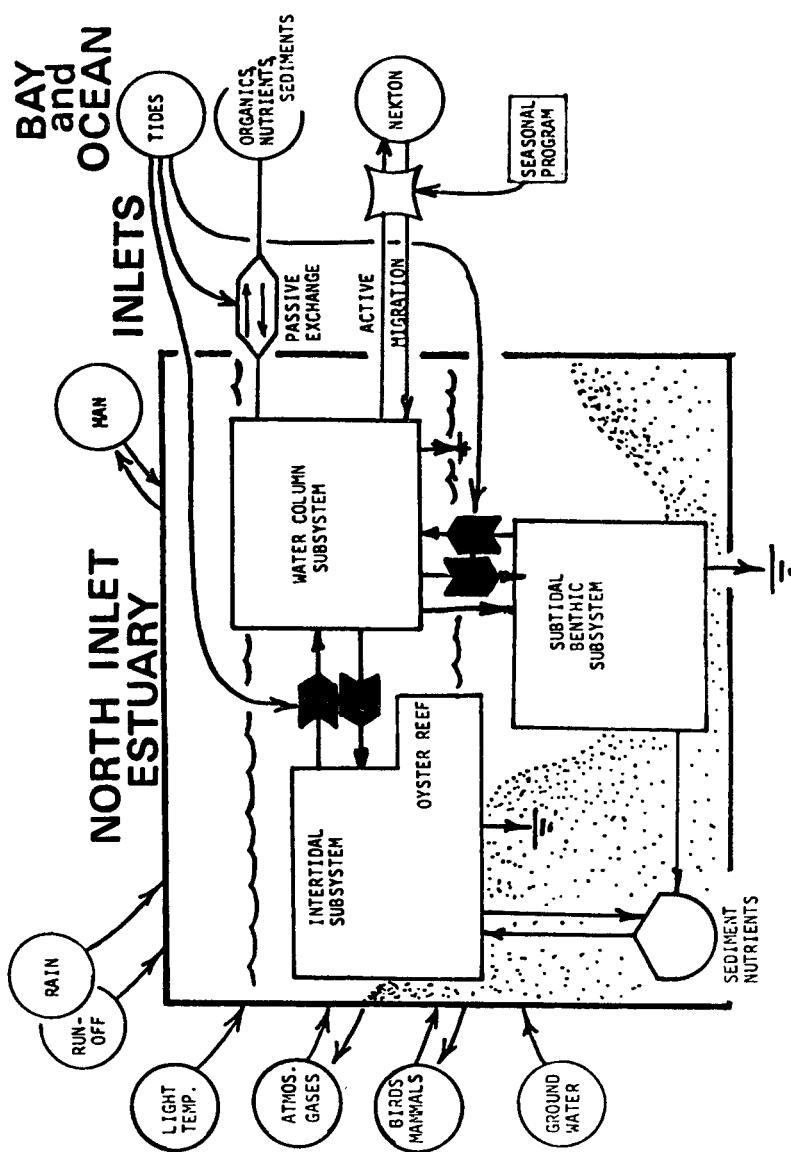
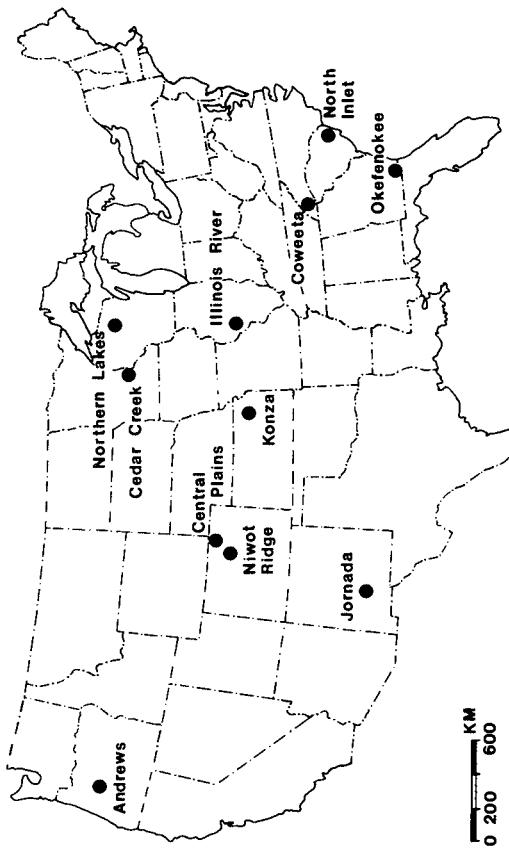


Figure 2.3: Location of the 11 LTER sites. H.J. Andrews (Coniferous forest, Oregon State University and US Forest Service); Cedar Creek Natural History Area (Hardwood forest, University of Minnesota); Central Plains Experimental Range (Grassland, Colorado State University); Coweeta Hydrologic Laboratory (Deciduous forest, University of Georgia and US Forest Service); Illinois and Mississippi Rivers (Large river ecosystem, Illinois Natural History Survey); Jornada (Desert, New Mexico State University); Konza Prairie Research Natural Area (Tallgrass prairie, Kansas State University); Niwot Ridge (Alpine tundra, University of Colorado); North Inlet (Coastal marine ecosystem, University of South Carolina); Northern Lakes (Northern temperate lakes, University of Wisconsin); and Okefenokee National Wildlife Refuge (Freshwater wetland, University of Georgia and US Fish and Wildlife Service)

Long-Term Ecological Research [LTER] Network



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are being addressed in relation to time as well as natural and induced stresses or disturbances.

1. Dynamic patterns and control of primary production.
2. Dynamics of selected populations of seed plants, saprophytic organisms, invertebrates, fish, birds, and mammals.
3. Patterns and control of organic accumulation (biomass) in surface layers and substrate (or sediment).
4. Patterns of inorganic contributions (atmospheric or hydrologic) and movement through soils, ground water, streams and lakes.
5. Patterns and frequency of apparent site interventions (disturbances) over space and time (drought, fire, windthrow, insects or other perturbations) that may be a product of, or induce, long-term trends.

Space restrictions do not permit a detailed discussion of the results of North Inlet LTER studies, but Table 2.1 lists the major ecosystem components being studied. The extensive long-term data base developed is available to investigators from other universities and institutes who want to study a specific research project for a short time, but whose results can be better interpreted within the context of a long-term data set. For example, is the short-term study being done during an unusually cold year?

CYCLIC CHANGES

In many estuarine systems, significant variation in landings of many commercial and recreational species have been reported. Declines in population size are typically attributed to overfishing, pollution, or man-made alterations to natural habitats. However, it is difficult to ascertain whether systematic declines in species' abundance have occurred and even more difficult to suggest testable hypotheses about cause-and-effect relationships that indicate whether natural and/or man-induced factors are influencing population variability. It is convenient and probably correct to assume that pollution is the population perturbator, but we need to have concrete evidence, not allegations. Studies of the population dynamics of species from a pristine environment would be extremely helpful in answering this question. Long-term studies of different species from North Inlet indicate that cyclic changes occur in the absence of man-induced changes.

MITIGATION

One of the many questions being discussed is that of mitigation. Is it possible and desirable to replenish and restore wetlands by creating new wetlands? This option may, for example, be considered in the case of an area where destructive processes have destroyed existing wetlands, or where a development project includes plans to destroy or dramatically alter existing wetlands and to replace them with new wetlands. Studies on wetland

Table 2.1: List of major ecosystem components

Primary production
<u>Spartina</u>
Phytoplankton
Population dynamics
Macrozooplankton and fishes
Meiobenthos
Oyster bed community
Fishes
Macrobenthos
Zooplankton
Barnacles
Chemical processes
Nutrient dynamics
Geochemistry
Physical oceanography
Sedimentology
Microbiology
Modeling
Statistics
Data management
Project director

dynamics can best be studied in a pristine environment, free from the overt influences of man-induced perturbations. To assess successfully the environmental worth of mitigation, it is necessary to know not only the structural aspects of transplanting plants but also the functional, dynamic attributes of this procedure. Even if the plants survive for a period of time and appear to be normal, how long does it take before the new area fulfills all of the normal functional activities of typical wetlands? Long-term studies in a pristine environment can provide the necessary data to answer these questions.

GENE POOL

A vital role of pristine estuarine environments is its capacity to provide stocks of plants and animals to repopulate estuaries which have been severely stressed and are attempting to recover. In addition to being a genetic reservoir for restorative activities, it is important in experimental studies in such fields as physiology, genetics, developmental biology, and toxicology to have access to experimental organisms from pollutant-free habitats. For example,

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embryological studies done on animals taken from PCB-contaminated waters may yield results which are markedly different from those on animals from pollution-free waters. It has been demonstrated that marine animals from regions of heavy metal contamination are functionally different from specimens from clean waters (Vernberg and Vernberg, 1974).

EDUCATION

An undisturbed estuary fulfills a demonstrated need to provide a field classroom where people can be educated about the structural and functional attributes of this valuable ecosystem. Educational programs at the North Inlet site involve the general public, school children from kindergarten through high school, undergraduate and graduate students, and teachers. In the future, as more coastal wetlands are altered, pristine environments will be of ever-increasing educational importance to society as demonstration sites of what our coastline once looked like.

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Chapter Three

AQUATIC ANIMAL PRODUCTION AND WETLAND RELATIONSHIPS: INSIGHTS GLEANED FOLLOWING WETLAND LOSS OR GAIN

R. Eugene Turner and Donald F. Boesch

It sometimes happens that, if the water is too clear, then the fish will no longer dwell there. When there are algae and water plants, fish can safely grow by hiding behind the plants.

(The Way of the Samurai Hagakure, pp. 26-7; translated by Minoru Tanaka; Sun Books, Albuquerque, New Mexico, 85 pp.)

INTRODUCTION

Wetland management is often confronted with controversy concerning the dependence of living resources on wetland habitats. The competing economic, aesthetic and recreational interests frequently disagree about the importance to living resources of incremental changes or modifications of wetland habitats. In a previous essay (Boesch and Turner, 1984) we discussed evidence of a relationship between the extent of wetland habitats and the yields of fishery species dependent on coastal bays and estuaries and reviewed the role wetlands may play in providing food and protection from predators. However, documentation of the effect on fishery stocks of loss or modification of wetland habitats has been poor. In this paper we assemble and examine accumulating evidence of this relationship, focusing primarily on penaeid shrimp stocks.

Penaeid Shrimp Life Cycles

Penaeid shrimp life cycles generally begin in the open sea as eggs which mature through naupliar, protozoal and zoeal stages. After drifting of the pelagic larval phases, the postlarvae enter estuarine areas on flood tides, and seek substrates, such as mangrove roots, to which they cling, until the next tide stage when they successively penetrate deeper into the estuary. Eventually they live a benthic existence while they grow in the estuary, an environment which offers food and refuge from predators. After several weeks or months, they move back into the ocean, but generally remain in shallow zones. Fishermen harvest them from the estuaries as postlarvae (for stocking ponds) or as subadults and adults in coastal waters. For reasons discussed below, most

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commercially important penaeid shrimp are considered to be estuarine dependent.

Shrimp Recruitment Relationships

Mortality in penaeid shrimp stocks is generally considered to be most severe in the larval stages and to decline with age. In many fisheries the variations in recruitment of an age group into the exploited stock is often directly related to the adult spawning biomass; but stock-recruitment relationships for penaeid shrimp are not clearly demonstrable (Garcia, 1983). That is, the adult stock size is determined by the changes in juvenile, even postlarvae abundance, not the reverse. So, variations in stock recruitment are not primarily the net result of changes in the adult spawning biomass.

However, there are causal relationships, with reasonable assumptions about them, between larval and juvenile abundances and the subsequent adult densities (Garcia and LeReste, 1981). Recruitment success is clearly dependent on climatic factors, predation levels, food supply, and habitat quality. Of these, the details of what constitutes quality habitat are not very precisely defined for penaeid shrimp. The relative significance of habitat is discussed here.

WETLAND AREA: STOCK-SIZE RELATIONSHIPS

Students of shrimp life cycles generally agree that recruitment of larvae from the spawning sites offshore into estuaries is very high; it is so high that post-larval growth and survival in the estuary are probably the most important factors affecting the harvestable adult population size (Garcia and LeReste, 1981; Garcia, 1983; Turner and Brody, 1983). Although estuarine salinity and temperature changes affect the annual potential for postlarval survival (discussed below), the long-term yields are linearly related to both the quantity and quality of intertidal habitat. Despite the difficulty in obtaining good measures of fishing effort and reliable catch statistics, we have several examples of this relationship throughout the world. Included here are site-specific examples from Australia, Malaysia, the Philippines, the northern Gulf of Mexico (Louisiana), and a general summary for the developed shrimp fisheries of the world (Table 3.1).

Jothy (1984) provided data from Malaysia for mangrove area and shrimp yields. Although the author does not describe the time period for the shrimp landings nor the amount of fishing effort, there is a clear relationship between shrimp landings and mangrove area in each of the states along Malaysia's coastline. Pauly and Ingles (1986) found a similar relationship in the Philippines. They had access to long-term data on both the artisanal and commercial trawl catches (these were combined in the data tables) and were able to reduce reporting biases in the catch and mangrove area estimates, the latter associated with economic interests concerned with the mangrove lumber concession. Staples, Vance and Heales (1985) investigated the habitat requirements of the juvenile stages

Table 3.1: Examples of positive relationships between penaeid stock sizes (reflected in annual harvests) and coastal wetland area within regions discussed in the text

Location	Range shrimp (mt)	Wetland (ha x 10 ⁻³)	Correlation coefficient (n)	Data source
Australia	0.2-1.5	0.1-0.8 ^a	0.76(6)	Staples <i>et al.</i> 1985
Malaysia	0-25	0-50	0.74(7)	Jothy 1984
Northern Gulf of Mexico	10-10 ⁴	1-10 ³	0.97(15)	Boesch & Turner 1984
Philippines	0.2-5	1-42	0.62(6)	Pauly & Ingles 1986

Note: a, For total length of mangrove lined rivers in each region

of five major commercial penaeid species in the general region of the Gulf of Carpentaria. Although they did not report mangrove area, the mean annual catch over 10 years was positively related to the length of mangrove-lined estuaries within the region and there was a statistically significant intercept near zero.

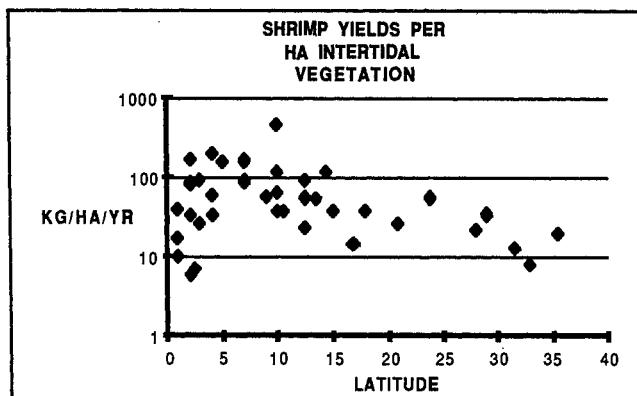
More complete and long-term data are available for estuaries in the northern Gulf of Mexico. The area of intertidal vegetation is also well known through several surveys since 1960. The landings from an estuary were positively and linearly related to the area of intertidal vegetation (Turner, 1977). Furthermore, offshore catches were correlated with inshore catches. In addition, the annual catch was related to the available area of intertidal vegetation with preferred nursery salinities for that year. There was no significant relationship between water surface area and landings. In addition, the species of shrimp caught are directly related to the kinds of intertidal coastal vegetation within that hydrologic unit. The same relationship between commercial harvests of penaeid shrimp and intertidal vegetation is found worldwide, although it changes with latitude, rising with decreasing latitude until around 5° N/S where it declines (Figure 3.1).

Other Fisheries

There are few attempts to relate river fisheries yields and wetland area. Risotto and Turner (1985) found a positive relationship of this sort for the Mississippi River (USA) when effort and latitude were included in the model. Welcomme (1979) surveyed the major river fisheries of the world and found several relationships between yield and channel length, discharge volume and floodplain size. He did not explicitly examine wetland area:yield relationships, but wetland area would be expected to vary positively with the factors he examined.

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Figure 3.1: The relationship between intertidal vegetation and penaeid shrimp yields from developed fisheries



Source: Modified and updated from Turner (1977)

STOCK LOSSES FOLLOWING WETLAND LOSSES

The above conclusions regarding wetland area and penaeid shrimp yields have been indirectly tested through large-scale changes in wetland area. Several examples have been documented with various degrees of success (Table 3.2). Examples like those of the Netherlands, where the entire estuary was blocked off and the fisheries collapsed (e.g. Boddeke, 1978) are not discussed since more than wetlands were altered.

Table 3.2: Summary of examples of penaeid shrimp stock changes following intertidal wetland changes

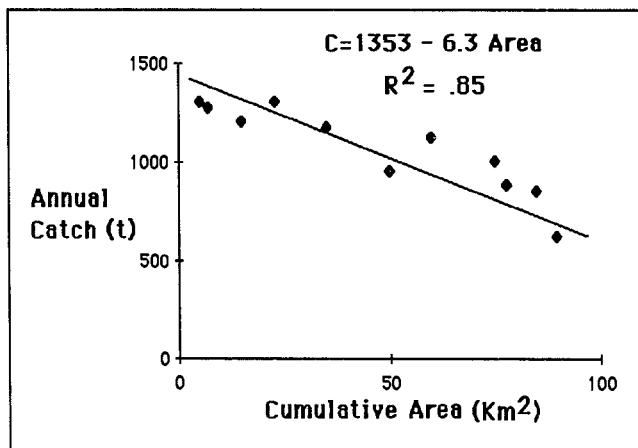
Area	Vegetation changes	Stock changes	Source
Louisiana	quantity, composition	quantity, composition	Turner unpublished
Kuwait & Saudi Arabia	quantity	quantity	Morgan & Garcia (1982)
Japan	none; mudflat reclamation	quantity	Doi <i>et al.</i> (1973)
El Salvador	quantity	quantity	Daugherty (1975)
Vietnam	quantity	quantity	Norman (1983)

Shrimp

In Japan, Doi, Okada and Isibashi (1973) showed that yields of Penaeus japonicus declined in proportion to land reclamation in the estuary (Figure 3.2). However, the intertidal land was not vegetated, but mostly shallow mudflats. Morgan and Garcia (1982) noted a long-term decrease in the recruitment of P. semisulcatus in Kuwait and Saudi Arabia which was not related to changes in effort, but probably to estuarine land reclamation. Mangroves in El Salvador were cleared for agriculture and the shrimp fisheries declined, although this analysis is far from complete due to the present difficulty in obtaining good landings and effort estimates (Daugherty, 1975). One result of the chemical defoliation of the southern coastal zone during the Vietnam war was the widespread loss of mangroves. Although the analysis is not generally available to the scientific community for review, there was apparently a severe decline in coastal fisheries stocks, including shrimp, following these losses (Norman, 1983).

In Louisiana, USA, the annual coastal wetland loss rate is presently about 0.8 per cent (Craig, Turner and Day, 1979; Turner, 1979; Turner, Costanza and Scaife, 1982). The changes in vegetation there are probably accompanied by a reapportionment of the catch among the estuaries in direct relation to the loss or gain of wetlands in that estuary, but the analysis is presently incomplete. There are changes in the composition of estuarine wetlands and shrimp. The wetland plants have become more salt-tolerant (as reflected in the species distribution) in the past 30 years with the decline in wetland area. Concomitant with this vegetation change has been an increase in the proportion of the catch made up of brown shrimp (P. aztecus) which requires relatively high nursery

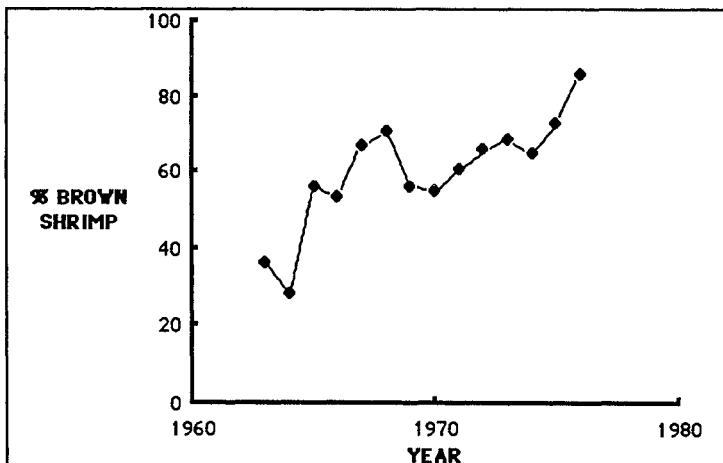
Figure 3.2: The decline of shrimp yields in Japan as related to the cumulative reclamation of intertidal lands



Source: Redrawn from Doi et al. (1973)

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Figure 3.3: The percentage of brown shrimp (Penaeus aztecus) caught in the inshore waters of Louisiana from 1963-76 (NMFS statistics)

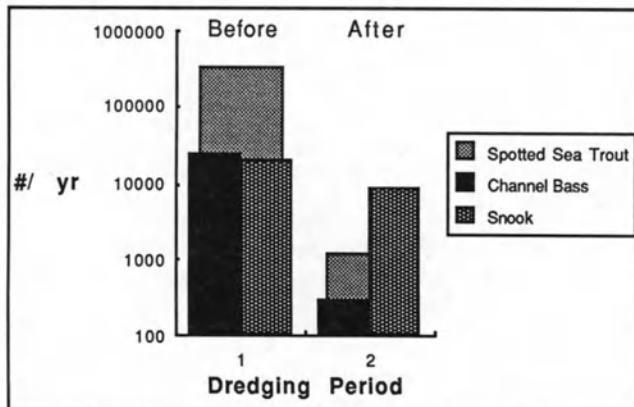


salinity and a decrease in the proportion of white shrimp (P. setiferus), which is more abundant in low-salinity nursery habitats (Figure 3.3). Studies following smaller-scale loss of wetlands have produced similar results. Adult shrimp densities declined when wetlands were blocked off from the estuary with levees or bulkheads (Mock, 1967; Trent, Pullen and Proctor, 1976).

Other Fisheries

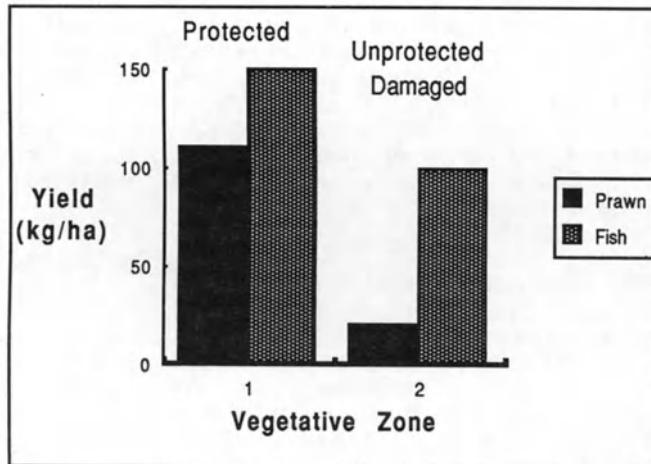
Woodburn (1961) and Krishnamurthy and Jeyaseelan (1980) examined the effect of alteration of wetland habitat and fisheries yields. Woodburn followed the apparent decline in fish harvest after wetland loss due to dredging in a Florida estuary (Figure 3.4). Although the data support the hypothesis that wetland area limits fisheries yields, one must cautiously interpret the data for three reasons. First, no records on fishing effort were reported; the decline in yields might well have been due to an uneven fishing effort. Second, the observed changes might be due to altered estuarine salinity, and climatic factors. Third, coincidental changes due to the dredging other than wetland loss may have caused the decline; the dredging occurred coincidentally with urbanization and probably increased estuarine turbidity. Krishnamurthy and Jeyaseelan (1980) reported fish and prawn yields from two nearby mangrove estuaries. One was protected and the other relatively disturbed by wetland loss, mangrove harvest and some pollution. Production was lower in the disturbed site (Figure 3.5). In addition to the three caveats mentioned in the Woodburn study, we have no information suggesting that the fisheries were similar in both areas before the wetland alteration. Both of these studies are interesting, therefore, but incomplete.

Figure 3.4: Fisheries changes in a Florida estuary following wetland dredging



Source: Adapted from data in Woodburn (1961)

Figure 3.5: A comparison of fisheries yields in two nearby Indian estuaries; one relatively protected and the other unprotected



Source: Adapted from data in Krishnamurthy and Jeyaseelan (1980)

Finally, the King George whiting fishery in Western Port, Australia, declined to about 20 per cent of that in the 1970s coincidentally with the loss of sea grass beds in the bay. The whiting uses sea grass meadows in the first three years of life (Robertson, 1977). Although fishing effort was reduced to 8-9

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boats compared to 20-25 earlier, the whiting is the highest valued fish and local ecologists report that the fishermen would be there if the whiting were present (D. Axelrad, personal communication).

STOCK GAINS FOLLOWING WETLAND GAINS

Most regions of the world are losing, not gaining wetlands. In a few instances, notably in coastal deltaic environments, there are local increases in wetland area. We are not aware of a study comparable to those discussed above on the impacts of wetland losses on fisheries resources. However, experimental studies, wherein wetland structure is increased, are beginning to appear in the literature. Some of these studies are discussed below.

Trent (1968) rehabilitated a marsh with Spartina alterniflora seeds and sampled monthly for penaeid shrimp juveniles and post-larvae from April to August. The seeded sample zone accumulated higher densities than the control sites indicating that the vegetation structure significantly (positively) affected habitat selection (Figure 3.6). Similar responses to experimentally increased vegetative structure are reported for freshwater bluegill (Lepomis macrochirus; Savino and Stein, 1982) and three species of lake bass (Micropterus spp.; Strange, Kittrell and Broadbent, 1982).

Some rather similar results are described by Kapetsky (1981) for coastal fisheries in China and Africa. Benin fishermen put out brush in the estuary and then fish around the 'brush-park.' These brush-parks accumulate fish or stimulate fish growth/production. There is a logarithmic increase in yield with a linear increase in branch number. Yield increases linearly with age. Equivalent brush-parks are used in west Africa, Madagascar, Sri Lanka and China, although the materials and fishing methods differ. The brush-parks offer habitat structure to the fish but do not materially add to the total food supplies. In light of the life history of the fish involved, the implication is that the increased habitat affords a refuge from predators.

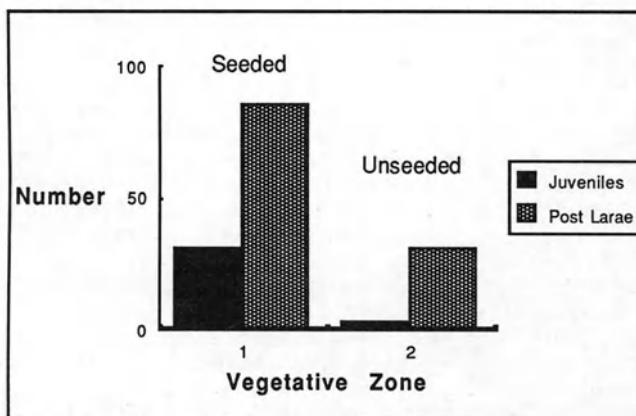
DIFFICULTIES INTERPRETING THE DATA

Among the numerous confounding factors complicating the interpretation of information such as reviewed here are changes in fishing effort, climate and coincidental factors varying as wetland area changes. The importance of considering fishing effort in analyzing fisheries data has been discussed previously and will not be mentioned further.

Climate

Adult shrimp and fish harvests may vary by as much as 100 per cent from year to year. The coefficient of variation in CPUE (catch per unit-effort) for the world shrimping fleet, by country, may be 20 to 90 per cent (Turner, 1986). Understanding the factors leading to this variation is important to fisheries management and to interpreting the relationship between yield and wetland area.

Figure 3.6: Changes in the density of shrimp in an estuarine control site and a site seeded with Spartina alterniflora



Source: Adapted from data in Trent (1968)

It is now well documented that these large annual variations are associated with changes in estuarine conditions when the juveniles are in the estuary. Variation in estuarine salinity and temperature are the best-documented climatic influences (Table 3.3), but the frequency and intensity of passages of meteorological fronts, river discharges of substrate conditions may also be important. Numerous data sets on catch per unit-effort are available (e.g. Gulland and Rothschild 1984; Kapetsky, 1981; Kapetsky and Lasserre, 1984a,b), but there is no systematic and comparative analysis of climatic influences. Copeland and Bechtel (1974) analyzed the salinity and temperature preferences of several penaeid species in estuaries of the northern Gulf of Mexico. They clearly demonstrated the interactive optimum preferences by shrimp for temperature and salinity, rather than linear relationships dominated by one factor.

Related Factors

In general, experiments in predator-prey interactions give similar patterns of interpretation as described in the preceding sections. For example, field and laboratory predator-prey experiments with *P. aztecus* in vegetated and non-vegetated salt marsh habitats indicate that small juveniles use the food-rich habitat among the stems to escape predators (Minello and Zimmerman, 1983a,b; Zimmerman and Minello, 1984; Zimmerman, Minello and Zamora, 1984). The number of predator attacks on prey and the percentage success of individual attacks declines with increasing vegetation complexity. Thus, the shallow wetland habitats appear to be favored sites as refuge habitats for juvenile shrimp; this is consistent with observations on organism adaptation to resource depression in the presence of predators (Charnov, Orians and Hyatt,

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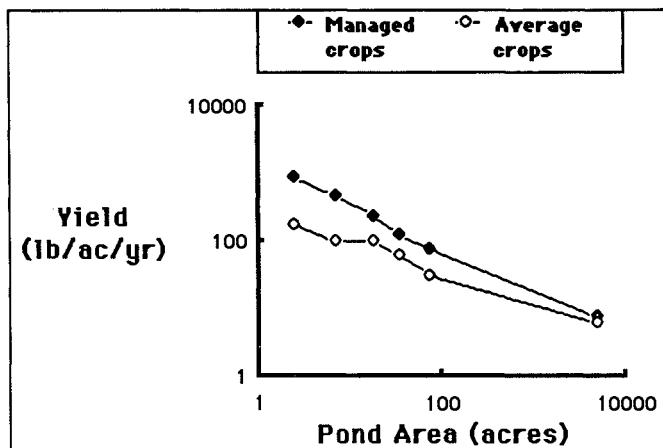
Table 3.3: Examples of the effects of climate on coastal penaeid shrimp stocks

Location	Species	Effect on yields	Source
North Carolina (USA)	<u>P.duorarum</u>	temperature(-)	Hettler & Chester (1982)
Louisiana (USA)	<u>P.setiferus</u>	salinity(-)	Barrett & Gillespie (1973)
	<u>P.aztecus</u>	riverflow(-)	Barrett & Gillespie (1973)
Louisiana (USA)	<u>P.setiferus</u>	salinity(-) temperature(+)	Turner (1979)
	<u>P.aztecus</u>	salinity(+) temperature(+)	
Northern Gulf of Mexico (USA)	<u>P.setiferus</u>	salinity(-) temperature(+)	Copeland & Bechtel (1974)
	<u>P.aztecus</u>	salinity(+) temperature(+)	
Florida (USA)	<u>P.duorarum</u>	water level(+)	Browder (1986)
Laguna Madre, Texas (USA; periodically hypersaline)	<u>P.fluviatilis</u>	rainfall(+)	Gunter & Edwards (1969)
	<u>P.aztecus</u>		
Australia	<u>P.merguiensis</u>	rainfall(+)	Staples et al. (1984) Ruello (1973)
Indonesia	<u>P.merguiensis</u>	riverflow(+)	Turner (1975)
	<u>P.monodon</u>		
Senegal	<u>P.duorarum</u>	salinity(+)	Le Reste (1980)

1976). These responses are also observed for freshwater lakes with wetlands fringing their borders, coral reefs, sea grasses and rivers (Groen and Schmulbach, 1978; Johannes, 1978; Savino and Stein, 1982; Strange, Kittrell and Broadbent 1982; Durouche 1985; Durouche, Provine and Kraal, 1984; Heck and Thomas, 1984; Holland and Huston, 1984; Robblee and Zieman, 1984; Hoyer et al., 1985).

The abundance of food obviously affects the survival and growth rate of individuals and populations. Energy, and material flow models of fisheries often imply that the harvest of adults is in some way proportional to primary production, 'new nitrogen,' or some other material. Virtually any aquaculture venture presumes food supplies limit yields. But, the relationship between food and

Figure 3.7: The relationship between fish harvest and land-water interface in ponds with and without additional food supplies



Source: Adapted from data in Maar *et al.* (1966) for east-central Africa

physical structure of habitat has not received much attention by wetland ecologists, particularly the modeler. Admittedly, habitat structure is a difficult parameter to introduce into any model, but we might ask how structure and material flows are related if we are to advance our understanding beyond single-limiting factor appreciation of populations. Maar, Mortimer and Van der Lingen (1966) provided fish yields from aquaculture ponds in east-central Africa. The average ponds were not managed, stocked, or manipulated but the fish were harvested annually. The managed ponds received additions of fertilizers to stimulate phytoplankton growth. Maar *et al.* (1966) demonstrated the increase in yield with increased management. An interesting pattern that appears when the size of the ponds is considered (Figure 3.7) is that there is far greater variation in yields related to the physical structure of the ponds than to the variations in management. The extent of edge habitat is inversely related to pond size with the same slope as shown in the figure. The implication is that the edge limits production without management and that food increases due to management amplify, but not limit, the potential yields. The same pattern holds for North American lakes (Turner, unpublished). We suggest that the pond edge is functioning for pond fish in the same way that wetland habitat support penaeid shrimp to result in the wetland:yield relationships discussed earlier.

CONCLUSIONS

Penaeid shrimp recruitment from larva to adult is influenced strongly by climatic events and habitat composition and quantity.

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The hypothesis that habitat quantity sets adult stock sizes is supported by limited field observations of predator-prey interactions, the direct relationships between yields and intertidal area, relative densities in disturbed and natural habitats, and by observations following wetland removal from the ecosystem. Conservation of habitat quantity is of high significance to sustained stock recruitment success since it seems to be the final determinate of natural potential stock densities which climatic influences annually modify. Other aquatic animals, notably fish, have life history and habitat attributes similar to shrimp; the implication is that many other fisheries are directly limited by wetland habitat.

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Chapter Four

RIVER REGULATION EFFECTS ON FLOODPLAIN HYDROLOGY AND ECOLOGY

Charles V. Klimas

INTRODUCTION

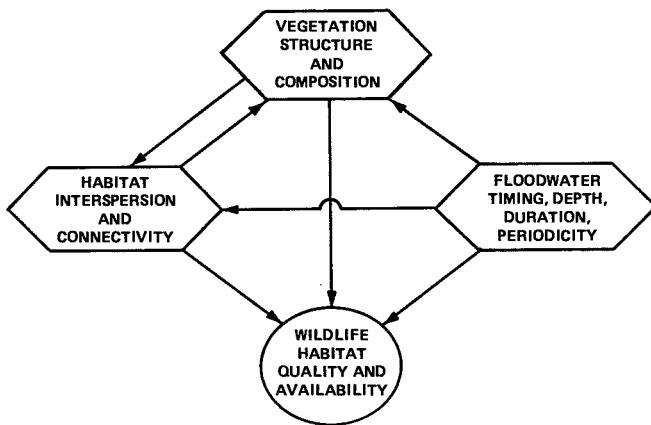
River engineering activities that modify floodplain hydrology induce basic changes in the character of floodplain ecosystems. These may include alteration of processes, natural communities, and land use patterns. This paper focuses on patterns of change that occur within floodplain forests (bottomland hardwoods) of the southern United States. Observations from these complex and productive systems are illustrative of interactions that occur in other floodplain ecosystems.

In practice, assessment of terrestrial ecologic impacts resulting from hydrologic change generally is accomplished using habitat-based wildlife evaluation. Direct and interacting effects of flood timing, depth, duration, and periodicity, vegetation composition and structure, and the spatial arrangement of habitats are all primary considerations in the impact assessment process (Figure 4.1). Various other important ecosystem components and processes are influenced by these factors and are thereby integrated to some extent in the basic wildlife habitat evaluation. These may include nutrient cycles, soil development, sedimentation, invertebrate production, ground-water movement, and interactions with aquatic systems. This discussion concentrates on the major integrating factors illustrated in Figure 4.1.

HYDROLOGY

The most distinctive characteristic of an undisturbed floodplain forest is its flooding regime. It is not the simple presence of water, but its dynamic nature that accounts for the high diversity and productivity of floodplain plant and animal communities. During flooding events, different forest types are inundated to varying depths throughout the landscape, permitting resource exploitation by wildlife species in patterns that change constantly as waters rise and fall (Fredrickson and Heitmeyer, 1986). Forest vegetation is similarly dependent on inundation and drainage patterns that differentially influence the ability of various plant species to establish and compete on a given site.

Figure 4.1: Interdependent factors that directly influence wildlife habitat quality



Given these patterns of resource utilization and community development, evaluations of altered floodplain hydrology should focus on aspects of flood timing, depth, duration, and periodicity. They should also recognize that certain floodplain sites are only secondarily influenced by river flooding (overbank and backwater) events: many sites are in sumps, on very poorly drained soils, or are directly associated with small tributaries, and are more frequently and directly influenced by local precipitation than river behavior. Major river hydrologic alterations will be discussed here according to the four general patterns described below.

1. **Stabilized** - This refers to any of a variety of changes that result in near-permanent inundation or growing-season saturation of substrates that formerly were periodically exposed. Typically this applies to areas within the permanent pools of reservoirs (Figure 4.2), but may include areas subject to pulses of growing season flooding (stable cycles) or permanently raised water tables, that prevent root-zone aeration.
2. **Shifted flood timing** - Lagged releases from reservoirs (Figure 4.2), constrained streams receiving increased tributary flows in response to storm events and similar systems can introduce floodwaters into a forest stand well into the growing season. Fall flooding may be imposed on wooded impoundments shallowly flooded in the dormant season to attract waterfowl (Figure 4.3). Though not directly related to river regulation in most cases, these greentree reservoirs are instructive regarding the effects of shifted flood timing.
3. **Increased flooding** - This category incorporates aspects of the previous two, but here refers specifically to relatively minor increases in flood duration, depth and periodicity. Typically, it includes moderate lag effects due to flood-control reservoirs

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Figure 4.2: Possible effects of a flood control reservoir over a generalized annual cycle. At various points these hydrographs illustrate raised and stabilized minimum water levels and increased, decreased and lagged flooding

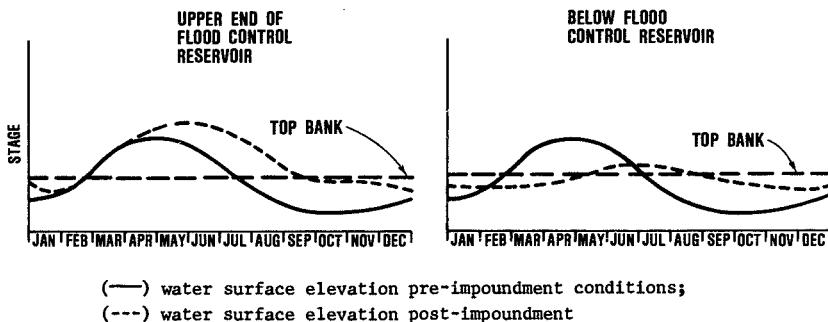
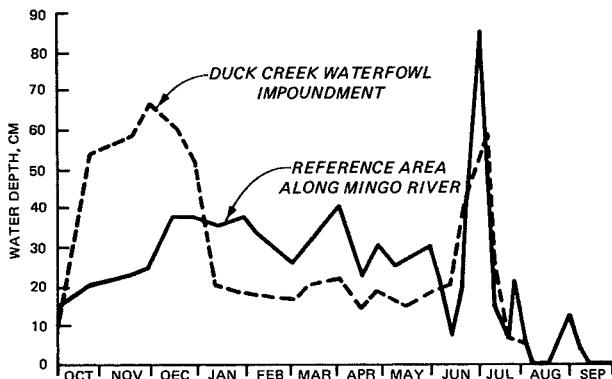


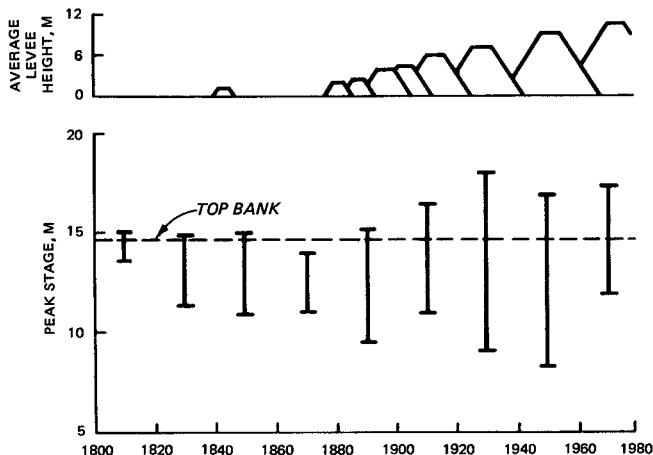
Figure 4.3: Depth of water on a greentree reservoir and a nearby floodplain area in Mingo Swamp, south-eastern Missouri, 1975-6



Source: Adapted from Fredrickson (1979)

- (Figure 4.2) as well as heightened flood peaks in levee-constrained floodplains adjacent to rivers (Figure 4.4).
4. Decreased flooding - As the principal objective of flood control projects, decreased flooding has influenced vast areas within floodplains of the southern US. Typically accomplished via reservoir operations (Figure 4.2), stream channel modifications, and levee systems, the effect is to reduce the frequency and duration of most flood events, although periodic severe floods may still occur (Petts, 1984).

Figure 4.4: Ranges of Mississippi River peak stages over 20-year periods at Natchez, Mississippi



Source: Adapted from Tuttle and Pinner (1982)

SPATIAL RELATIONSHIPS

Where overbank and backwater flooding have been sufficiently reduced and drainage systems are installed many floodplain sites have been cleared for agriculture (Turner, Forsythe and Craig, 1981). In addition to the overall reduction in forest lands, however, more subtle impacts may occur that relate to the pattern of agricultural conversion. Typically it is the less-frequently flooded sites that are cleared, whereas pockets of relatively wet sites remain scattered across the landscape, or form a continuous corridor directly adjacent to the river. The result is a pattern of differential reduction of certain forest types and a general fragmentation of the relatively wet sites that remain in poorly drained or frequently flooded areas. The spatial arrangement and size of forest fragments are increasingly recognized as important components of wildlife habitat quality (Burgess and Sharpe, 1981). In addition, there is a related problem that concerns vegetation; many heavy-seeded plant species (*Carya*, *Quercus* spp.) are partly dependent on animal activity to assure seed dispersal, particularly where flooding has been eliminated as a dispersal mechanism. Potential problems arising from this are discussed further below.

Although flood reduction may cause fragmentation and isolation, it may also have other spatially related effects that should be considered. Chief among these is the interspersion of croplands that serve as a reliable food source for many wildlife species. Habitat-based wildlife evaluation systems generally take a realistic view of this situation, and attempt to recognize proximity to grain and legume crops as an addition to habitat value for many wildlife species.

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Increased flooding may also influence landscape pattern by making some areas unattractive for farming. Figure 4.4 illustrates the steady rise in flood peaks within the confined floodplain of the Mississippi River over the last five decades. This increase in flood depth and frequency has evidently contributed to the preservation of the forested river corridor that traverses the length of the lower Mississippi Valley, passing through large expanses of relatively denuded floodplain. On a smaller scale, isolated areas unsuitable for agriculture may occur in conjunction with various impoundments.

VEGETATION

Wildlife habitat evaluations rely on vegetation characteristics as a primary determinant of habitat quality. An extensive body of research has established the strong relationship between floodplain forest composition and hydrology. Generally, these relationships are expressed in terms of species' tolerances to flooding, and tolerance zones have been designated that provide a sound model for examining the distribution of relatively undisturbed forest communities along the flooding gradient (see, for example Bedinger, 1971; McKnight, Hook, Langdon and Johnson, 1981). These studies provide considerable insight on the eventual forest communities that might be expected to develop in response to a change in hydrology. Intuitively, one anticipates a shift to a better-adapted forest type where flooding has been somewhat decreased or increased. However, a realistic assessment of the community replacement process should focus on more than simple species' flood tolerance.

The various hydrologic alterations that may be imposed on floodplain ecosystems can be categorized as either being consistent with, or departing from hydrologic cycles that may occur naturally elsewhere in the floodplain. Moderate increases and any decreases in flood duration, frequency, and depth represent changes in the capacity of the site to support particular plant species, but generally do not eliminate forest cover. However, certain types of hydrologic changes interfere with critical stages in species' life histories; in effect, they depart from natural patterns sufficiently that no, or very few, species are adapted to the conditions imposed.

The extreme example of this is the raised and stabilized water levels of reservoirs. Few mature trees can survive permanent inundation and reproduction is precluded for all species. Numerous studies have quantified tolerances to permanent flooding as well as water-related limitations on germination and establishment for many floodplain tree species (for review articles see Teskey and Hinkley, 1977a, b; Whitlow and Harris, 1979; and Hook, 1984). These studies indicate that it is periodic, prolonged lack of submergence that allows establishment of most species while mature trees require adequate root-zone aeration. Since late-season floods impact seedlings too soon to allow establishment, their overall effects on long-term stand development are similar to permanent flooding, although deterioration of existing stands may proceed

more slowly. An important exception to the general pattern of stand mortality involves bald cypress (Taxodium distichum) and tupelo (Nyssa aquatica). Established stands may deteriorate if permanent inundation is imposed, but they can persist for many decades (Klimas, 1986) and may be partially rejuvenated or replacement stands established using well-planned periodic drawdowns.

The imposition of lagged or shifted flood events may have similar results, especially if they are recurring (annual) events or involve mid-growing season (warm water) flooding. Even dormant-season floods that occur at unusual times are potentially detrimental to forests. Studies of greentree reservoirs (Fredrickson, 1979; Newling, 1981; Francis, 1983; Schlaegel, 1984) indicate a long-term pattern of increased mortality, reduced growth, reduced mast production, and compositional shifts to less-desirable forest types as well as less-obvious effects such as depressed invertebrate production (Batema, Henderson and Fredrickson, 1985). Again, the problem seems to derive partly from the stability of the water regime. Newling (1981) suggests a rotation system to allow individual greentree units to 'rest' periodically, thus greatly slowing the rate of stand decline.

Under undisturbed conditions, periodic flooding influences species composition primarily through differential seedling mortality. This process defines the potential species complement for a given site, but subsequent stand development involves complex competitive interactions. Various soil and site factors, including flooding, influence species' growth rates and thereby differentially favor species with respect to the attainment of canopy positions. Shade tolerance, longevity, the periodicity of seed production and seed dispersal strategies also affect success (Noble and Slatyer, 1980). The relative influence of each of these factors may be greatly changed by forest management practices.

Given the above, an increase in overall 'wetness' of a site that is insufficient to cause mature tree mortality would have fairly predictable results. As flood duration, depth and frequency increase, the number of species adapted to the site decreases. Propagules of adapted species should arrive at sites subject to overbank flooding quickly if the species exist upstream, as seeds of very flood-tolerant species are readily water-borne (Fowells, 1965). Seed source sites will generally be available since land clearing efforts in floodplains focus on drier sites. Delays or reduction in seed availability, as well as harvest practices will greatly influence stand composition and structure, as discussed further below, but in general, the overriding influence of flooding allows direct application of various flood tolerance ratings in predicting eventual community composition. This fairly high degree of predictability is demonstrated in the increasing application of forest stand modeling to the evaluation of impacts of increased flooding (e.g. Brody, Pearlstine, Conner and Kitchens, 1986).

Decreasing site inundation involves more complicated considerations than does increased flooding. Direct adverse effects on wildlife (particularly waterfowl) are fairly obvious, but changes in vegetation are difficult to anticipate. Generally, no immediate mortality is induced, and subsequent shifts in composition proceed

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slowly. In the absence of harvest and where seeds of appropriate species are present, a very gradual shift in composition would be expected (Figure 4.5a). Seedlings of less flood-tolerant species would no longer be eliminated by periodic prolonged flooding. Slower-growing species typical of wet sites (e.g. *Quercus lyrata*) would gradually be replaced by faster-growing species of drier sites (e.g. *Quercus nuttallii*) as canopy openings become available and if soils are appropriate. The long-term effect would probably be to increase stand species diversity, and overall landscape diversity would also be increased if the topography is such that pockets of very poorly drained sites remain scattered throughout the forest.

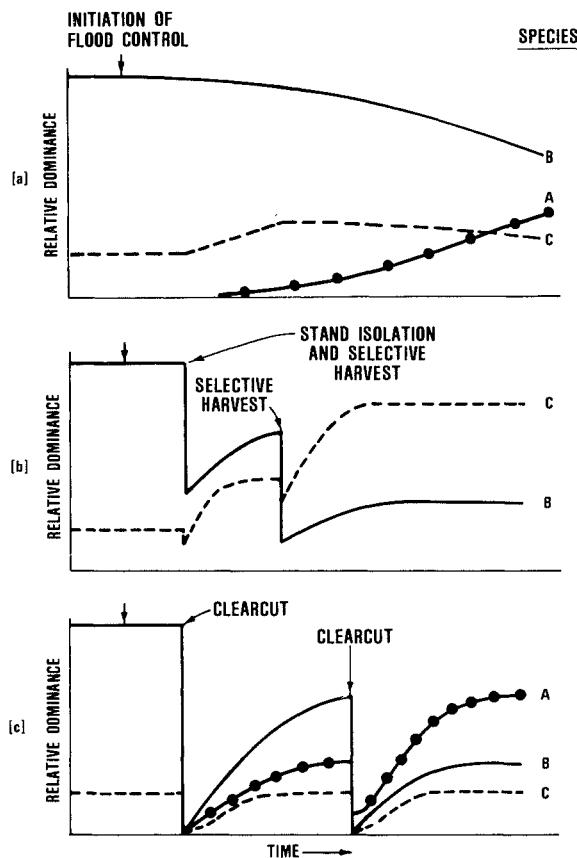
This simple replacement pattern is unlikely to occur in many areas of the south. Forest management and land-clearing practices impose stresses that overwhelm the subtly shifted competitive balance described above. Conversion to agriculture, as indicated earlier, is centered on the drier floodplain sites, therefore stands where flooding has been reduced are prone to become isolated, and restricted in size if not eliminated altogether. Since the best-adapted species complement may not be present on site at the time of flood reduction and isolation, seed source may be a significant problem. This situation can potentially be greatly aggravated by abusive harvest practices, which may target commercially valuable trees (*Quercus* spp.) while leaving a residual stand of less desirable, but broadly shade- and flood-tolerant species (*Ulmus*, *Celtis* spp.). This scenario, where isolation and mismanagement favors development and persistence of a degraded forest, is illustrated in Figure 4.5(b).

Just as influences not directly related to flood reduction can divert forest development to a degraded, stagnant condition, they also can be employed to speed transition of the system to the better-adapted (more productive) composition described earlier. Figure 4.5(c) shows a hypothetical management approach that prevents the process shown in Figure 4.5(b). Here, the forest has not been isolated from appropriate seed sources. Continuous cover or forested corridors remain between the site and nearby uplands and other floodplain forest types. The harvest strategy employed (clearcutting is used in this example, for clarity) does not leave an advanced residual stand of broadly tolerant species, and therefore favors more desirable species (*Quercus* spp., *Fraxinus* spp., etc.). As seeds of the better-adapted species become common on the site, and carefully prescribed management practices continue, composition shifts to stabilize at a point where overall productivity, diversity and mast production are maximized. This simplistic three-species example is intended only to illustrate the processes under discussion: the actual management strategy for a given site may be very different. In all cases, however, the objective would be to suppress or prevent capture of the site by species that can tolerate a wide range of light and flooding conditions, while encouraging recruitment of long-lived, more valued species. Accomplishing this is an uncertain process under normal circumstances (Johnson, 1978; Bowling and Kellison, 1983; Gresham, 1985), and the added complication of isolation and flood

reduction dictates that extremely attentive and skilled management may be required on many sites.

Figure 4.5: Three hypothetical scenarios for forest stand development following flood reduction. Species A is a preferred species that is relatively intolerant of flooding and is not present in the original stand. Species B is a very flood-tolerant preferred species that dominates in the original stand. Species C is a broadly shade- and flood-tolerant species adapted to the old and new flooding regimes but not a preferred lumber or wildlife species.

(a) Illustrates a slow shift in species composition in the absence of harvest and stand isolation. (b) Shows severe stand degradation resulting from the cumulative impacts of stand isolation and high-grading in addition to altered hydrology. (c) Illustrates one possible stand and landscape management approach that accelerates transition of the stand to a composition adapted to the new flooding regime.



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SUMMARY

Changes in hydrology that result in stabilized water levels or shifted timing of floods may depart too drastically from any natural cycle to permit an adapted forest community to remain or develop on the site. Changes that result in non-catastrophic shifts in flood frequency, duration, etc. may mimic flooding regimes that occur elsewhere on the landscape, and gradual shifts in forest type would occur if the system was otherwise undisturbed. In reality, however, floodplain forests are subject to clearing and exploitation, which are facilitated by flood reduction and inhibited by flood increases. These activities can act as additional impacts on the hydrologically altered system, resulting in degradation and stagnation of the forest. On the other hand, careful maintenance of forested corridors linking various component floodplain systems, and management designed to promote rapid transition of hydrologically altered areas can increase overall productivity and benefit wildlife populations. The loss of shallow floodwaters within the forest represents a major impact on many wildlife species, and should receive special consideration in evaluating the impacts of activities that will reduce flooding.

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Chapter Five

EXPERTISE IN WETLANDS RESEARCH AND MANAGEMENT: THE NEED AND SOME PRIORITIES FOR NORTH-SOUTH TRANSFER

Patrick J. Dugan

INTRODUCTION

For many years now wetlands conservation has been a high priority for a wide range of conservation groups in the more developed world. However, while in recent years the international attention of these same groups has focused upon the dramatic loss of the world's tropical forests, remarkably little attention has been directed to the alarming rate of wetland loss in the developing world. Yet ironically it is there, and especially in the tropical regions where human societies depend most closely and most heavily on wetlands, that a rapid and substantial increase in the wetlands conservation effort is urgently required.

Fortunately, recent progress has been made in this domain. In particular, the International Union for Conservation of Nature and Natural Resources (IUCN) has, with the substantial support of World Wildlife Fund (WWF), initiated a major international program for wetlands conservation (WWF, 1985). However, it is a basic premiss of this initiative that global wetlands conservation is a field where a wide range of governments, organizations, individuals and disciplines have an important role to play. The principal aim of the IUCN Wetlands Program (Maltby and Dugan, 1985) is, therefore, to act as a catalyst and stimulate this wider involvement in international wetlands issues.

There is no doubt that resolving the wetlands conservation problems of the developing world will require a major commitment and investment by governments and the development assistance community. However, this alone will be insufficient to achieve the rapid progress required. If this is indeed to be realized, the conservation and scientific community in the developed world will need to make a major effort to apply its experience to exploring, and helping to find solutions to, the problems of wetlands conservation in the tropics. It is the purpose of this paper to explore a number of areas in research and management where such transfer of technology and experience is most urgently required, and suggest means by which such transfer can be achieved.

WETLANDS RESEARCH

The Problem

A brief glance at the scientific literature provides impressive testimony to the large quantity of research which has been carried out on wetlands in North America and Europe. Yet despite this large volume of published material it is salutory to recall that the scientific case for wetlands conservation is still based largely upon what is a very basic understanding of the hydrology and ecology of most wetland ecosystems. Given that this is so in the developing world, it is hardly surprising to note that the scientific base for wetlands planning decisions is especially limited. Only in a few countries, e.g. Kenya and Brazil, has up-to-date wetlands research been carried out, and much of this has little relevance to the immediate needs of wetlands conservation. Accordingly, it is not surprising that most decisions affecting wetlands are made in the absence of any strong conservation case. Conversely, it is extremely difficult to convince governments and development assistance agencies of the value of innovative wetlands conservation initiatives, when the case for doing so is based largely upon hypotheses.

Given these considerations it is clear that there is an urgent need for a major increase in applied wetlands research in the developing world, and especially in the tropical regions. However, as we consider wetlands priorities for the developing world, and especially the way by which wetlands scientists in the developed world can best help address these priorities, there are two points which should guide our thinking.

1. It is most important that the considerable body of knowledge that already exists for the temperate regions of the world, and the experience gained in obtaining this, be examined to determine how such data, and especially that experience, can help guide future research in the tropics.
2. Given the current rate of wetland loss and the threats which currently hang over the wetlands of the developing world, it is essential that the conservation and scientific communities adopt a very pragmatic approach when considering wetlands conservation needs. Consequently, almost all tropical wetlands research should be of immediate relevance to problems which are already clearly identified, and to which answers are urgently required. To do otherwise will have little impact on the current rate of wetland loss.

The Priorities

Given the above considerations, eight major priorities for conservation-oriented wetlands research in the developing world can be identified.

- (1) Wetlands assessment. It is now widely recognized that creation of protected areas cannot alone save wetlands and the services they provide to human society. To achieve this goal, human use of wetlands needs to be regulated through local, national and inter-

THE RESOURCE

national legislation. Yet while in both Canada and the USA there are major efforts underway to develop national programs for wetlands assessment, our ability to do anything comparable for any country in the developing world is very poor. Accordingly much greater attention needs to be devoted to establishment there of national or local programs of wetlands assessment. In doing so, the experience gained in North America will be of crucial importance. Only by building upon the lessons learned will the necessary tools be rapidly and effectively developed. The assessment techniques and procedures developed will of course be crude. But only by having these available and by testing them in tropical situations will a more refined system be developed.

(2) Hydrology and wetland productivity. Wetland quality depends closely upon the quantity and quality of water available. Yet most decisions on dam construction and river embankment are made with little thought to their impact upon the productivity of the river's floodplain. A series of detailed case studies which examines such impacts will provide a most important tool in presenting to governments and aid agencies the argument for integrated management of river basins and their associated wetlands.

(3) Water quality. It is well known that wetlands can play an important role in regulating water quality. Yet, at present, almost all quantified data come from the United States. Accordingly there is a major need to determine the precise role that wetlands in other regions, especially the tropics, play in filtering pollutants especially from non-point sources.

(4) Fisheries. One of the major values of wetlands is the high fish production of most sites. Many floodplains and coastal zones are important breeding and nursery areas, whereas many lakes and rivers provide locally or nationally important fish yields. Yet as efforts expand to exploit these floodplains and coastal zones for agriculture or aquaculture, the impact upon the fish populations has in many areas been catastrophic. Nevertheless it is clear that until a solid argument based on hard scientific data is made for maintenance of specific sites or types of habitat within floodplains or mangroves, this effort is likely to continue. There is therefore an urgent need in many areas of the world for more detailed study of the importance of wetlands in fish production and of the economics of wetland restoration for agriculture and aquaculture.

Similarly, in many parts of Africa, small-scale fisheries provide a major contribution to the diet of rural communities. Yet these are currently given little treatment in fisheries development projects. And in many parts of the Sahel the recent drought has led to serious over-exploitation of the fishery resource. Accordingly there is a major need to develop programs of fishery conservation and exploitation which are based upon a sound knowledge of the needs of rural people and of the population dynamics of the fish species concerned.

(5) Sustainable use of wildlife populations. Although the species diversity of wetlands is not particularly noteworthy, there are

many species which occur in large numbers and have been used traditionally by local communities as a source of food and income. However, many of these populations are, as a result of over-exploitation today, threatened with local extinction. Yet in many areas maintenance and sustainable utilization of these wildlife resources is the principal justification for maintenance of the wetlands. There is therefore an urgent need to expand research into the levels and systems of utilization which can be sustained by these species.

(6) Peatlands. In the past decade the combined pressures of rising oil prices and demand for agricultural land have led to the mining and subsequent cultivation of many of the world's peatlands. Until very recently, however, this was largely confined to the temperate zone. Now, however, technological advances have rendered possible the extraction of tropical peats for conversion into fuel. As a result there are now major plans to exploit many of the world's tropical peatlands, especially in south-east Asia. The rush to exploit this resource is viewed with concern by the conservation community. Yet our understanding of the likely impact is very poor. We only note that loss of temperate peats has had major hydrological impacts and fear that similar impacts will be of greater magnitude in the humid tropics. Accordingly there is a major need to expand our understanding of the hydrological and ecological roles played by tropical peatlands.

(7) Traditional human use of wetlands. It is increasingly widely recognized that as the conservation and development communities seek to promote sustainable development of the earth's natural resources, many of our efforts would benefit from a more thorough appreciation of traditional forms of land use. Nowhere is this more true than in many of the wetland regions of Africa where one of the major reasons for current levels of environmental degradation is the breakdown of traditional systems of land management. As efforts intensify to conserve these wetlands resources it is essential that these can benefit from a more thorough understanding of how this breakdown of traditional controls on land-use has increased the rate of habitat loss, or how maintenance of traditional practices have prevented loss.

(8) Land-use planning. One of the arguments for maintenance of natural wetlands is that most forms of modification to the system are not sustainable in the long term. Yet the decision to modify a wetland, or leave it untouched, depends upon a thorough understanding of the hydrology, pedology and agricultural potential of the site. Accordingly, development plans for wetland areas should be based upon a detailed study of these elements as well as of the wildlife, fisheries and agricultural status of the natural site.

Some Solutions

The list of research areas outlined above is indeed long. However, there are a number of ways through which the scientific community in the developed world can help address these problems. The first

THE RESOURCE

of these, and the simplest, is for wetlands scientists in North America and Europe to devote greater attention to wetlands overseas. Funding sources exist, either via development assistance agencies, private foundations, or the more traditional sources of research funds, to carry out field research on wetlands problems in the developing world. Yet much greater emphasis needs to be placed by the scientific community upon seeking these funds and upon using them to address conservation priorities.

However, while direct pursuit of wetlands studies by more developed country researchers is essential in many countries of the developing world, a more effective means in others lies in assisting appropriate nationals to pursue their own research. This is especially true in many countries of Latin America where there is a large body of well-qualified biologists capable of pursuing a wide range of research activities. In particular, universities and other research groups in Europe and North America should:

1. seek to develop closer ties with these developing country scientists through improved communication of research results and techniques;
2. help to establish opportunities for students and researchers from these countries to work and study with them, thus learning of the methodologies and techniques which might be applied to their own tropical problems. This might take the form of studentships or especially working vacations where researchers, for only the cost of expenses, could work with appropriate institutions during vacation months.

WETLANDS MANAGEMENT

North - South

The conservation communities of Europe and North America have led the world in establishing wetland reserves, and in establishing techniques for their management. As the wetlands conservation needs of the developing world are identified, the expertise available in the more developed countries can play a major role in designing appropriate management. Thus, while it is uncertain whether the precise techniques used in wetland management learned in Europe or North America are of direct relevance to the tropics, the experience gained in these northern countries is invaluable in assisting tropical wetlands managers to pose questions, and design appropriate responses to the array of management problems they face.

Already a number of organizations in North America, in particular the US Fish and Wildlife Service, the US National Park Service and WWF-US have been very active in developing training courses for natural resource managers from Latin America. However, this effort needs to be expanded and take much greater account of the special problems of resource management and institutional integration posed by wetlands conservation. Similarly a number of groups, in particular the International Waterfowl Research Bureau, are engaged in the training of wetlands managers in Africa. However, here again, much greater efforts are required

to expand this work, especially through training courses held in Africa. Conservation groups in Europe and North America can greatly assist in developing these activities, not only by direct funding, but also by making available appropriate technical expertise to teach such courses.

South - South

When considering transfer of experience and technology to address the needs of the developing world, there is a marked tendency to think only in terms of North-South transfer. Yet while the majority of wetland research and management institutions are indeed in the North, there are clearly severe limitations to the extent to which management practices in temperate regions can be applied to the problems of the South. Thus, in considering the issue of technology transfer for wetlands management, it is essential that much greater attention be given to the role of South-South transfer. For example, the expertise and experience now available in Taiwan or Thailand is of much greater relevance to the mangrove management problems of Latin America or Africa than is expertise and experience available in Europe and North America. Yet such expertise is rarely used, often with environmentally damaging consequences. As the wetlands conservation community begins a major drive for wetlands conservation in the developing world, it is of great importance that much greater use is made of such appropriate expertise.

CONCLUSIONS

The thesis of this paper is that as efforts increase to address global problems of wetlands conservation there is an urgent need for increased exchange of experience and expertise in research, especially from the countries of Europe and North America to the countries of the developing world, while in management both North-South and South-South exchange is needed. This requires that two questions be asked by all involved in wetlands conservation and research. First, how can our work be made more relevant to the needs of global wetlands conservation? And secondly, how can we best help provide our experience and expertise to the needs of the developing world? The answers to these questions clearly depend upon the work of the people involved and the nature of the institution concerned. However, these qualifications notwithstanding, there are a number of general conclusions which are applicable to most situations.

1. All institutions concerned with wetlands research or management should examine how they can most effectively contribute to an exchange of expertise and experience which will help address the needs of global wetlands conservation.
2. Such institutions, and in particular universities and research stations in Europe and North America, should seek to expand the opportunities through which students and researchers from Latin America, Africa and Asia can work with them, thus

THE RESOURCE

- learning of the methodologies and techniques which might be applied to their own tropical problems.
- 3. All wetlands researchers should consider how their own work might more directly contribute to the needs of wetlands conservation, especially in the tropics, and seek to find funding for such work.
 - 4. In all cases such research should seek to include a training component, thus expanding the experience of developing country researchers. The training should not only cover technical and scientific data, but also management and institutional elements.
 - 5. Conservation groups in the developing world should examine the ways through which they can best contribute to the training needs in wetlands conservation. This might include establishment of training courses, strengthening existing training centers, or simply provision of experts.
 - 6. These training activities should include not only technical and scientific considerations, but deal also with the special inter-institutional cooperation required for effective wetlands conservation.
 - 7. All governments and development assistance agencies should, where appropriate, seek to encourage use of developing country experts in planning and implementing wetlands conservation and development projects in Latin America, Africa and Asia.

ACKNOWLEDGEMENTS

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PART II

HYDROLOGIC AND WATER QUALITY VALUES OF WETLANDS

Chapter Six

A REVIEW OF THE RECHARGE-DISCHARGE FUNCTION OF WETLANDS

D.I. Siegel

INTRODUCTION

The recharge-discharge function is an important but complicated part of wetland hydrology (Adamus and Stockwell, 1983). Ground-water discharge can maintain a high water table in wetlands, whereas recharge to the underlying aquifers can replenish ground-water supplies. However, the methods previously employed to determine ground-water flow in wetlands by indirect estimation are inadequate. The inherent error involved in measuring the various factors in a water budget is so high that the volume of ground-water flux cannot be accurately determined indirectly as a residual (Winter, 1981). 'Average' gradients on the water table often cannot be used to determine the major directions of ground-water flow because of the build-up of transient water-table mounds which temporarily reverse flow directions at wetland margins (Anderson and Munter, 1981; Winter, 1983). Most recent advances in understanding the recharge-discharge functions of wetlands have been obtained by using the hydrogeologic systems approach of ground-water study to wetland environments.

The purpose of this paper is to review our current understanding of the recharge-discharge function with respect to this approach, with an emphasis on northern wetlands covered by thick accumulations of peat. A complementary review of the function for wetlands not underlain by thick peat can be found in Chapter 7.

BACKGROUND

Hydrogeologic systems approach

The hydrogeologic systems approach, described in detail in textbooks on hydrogeology (e.g. Domenico, 1972; Freeze and Cherry, 1979), involves the complete description of the geologic framework and hydraulic boundaries of ground-water flow systems of which wetlands are a part. The ground-water system is conceptually and mathematically constrained by the material properties of the porous media, topography of the water table, and a combination of no-flow, hydraulic potential, and flux boundaries. The directions of ground-water flow and the distribution of hydraulic potential in

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space and time are described by partial differential equations, which are solved analytically, numerically or graphically.

Studies using the hydrogeologic systems approach have shown that ground water at any given location occurs in discrete flow systems that are constrained by their spatial dimensions and hydrogeological setting (Toth, 1963; Freeze and Witherspoon, 1967). Ground water in local flow systems is recharged at topographic highs on the water table and discharged at adjacent lows. Intermediate-scale flow systems discharge beyond adjacent areas of low elevation of the water table. Ground water in regional flow systems is recharged at regional topographic divides and discharged at major river systems or lakes.

Ground-water flow in organic soils

The hydrogeologic systems approach has not been generally used in wetlands underlain by thick deposits of peat because the pore water in peat is commonly assumed to be divorced from the water in underlying mineral soils. This assumption is based upon field and laboratory studies (reviewed by Chason and Siegel, 1986) that determined the hydraulic conductivity (K) of humified peat (cato-telm, *sensu* Ingram, 1967) at about 1 m depth to be orders of magnitude smaller than that of the upper 0.5 m of fibric peat (the acrotelm, *sensu* Ingram, 1967). Recent studies have shown that the K of humified peat at depths greater than 1 m can be hundreds of times greater than previously assumed (Chason and Siegel, 1986), probably because of discontinuities in the peat column that cause pipe-like flow (e.g. Jones, 1981).

Low hydraulic conductivity of peat does not indicate that pore water in peat is divorced from that in underlying mineral soils. The physics governing ground-water flow in peat is the same as that governing flow in mineral soils (Hemmond and Goldman, 1985). Wetlands are mostly located on glacial moraines, lake beds, fluvial backwaters, and marine estuaries which are commonly underlain by fine-grained inorganic sediment with similar hydraulic conductivity (Freeze and Cherry, 1979). Ground water in peat is not hydraulically disconnected from the ground water in underlying mineral soils. Peat is simply the upper layer of a continuum of porous materials through which ground water moves; and it is subject to the same scale dependency (Bear, 1972) and anisotropy of material properties as any other porous media.

The interaction between water in peat and mineral soils is particularly significant in the evolution of very large peatlands. It is often assumed that water-table mounds under raised bogs are not influenced by the regional water table (Ingram, 1967). Theoretical studies on ground-water flow using the hydrogeologic systems approach have shown that, in fact, water-table mounds that underlie raised bogs (Siegel, 1981; Ingram, 1982; Almendinger, Almendinger and Glaser, 1986) are persistent recharge areas for the surrounding fens and regional water table (Siegel, 1981; Siegel, 1983; Boldt, 1986). Surface-water chemistry and vegetation communities are profoundly affected and perhaps controlled by the small amounts of ground-water discharge at bog margins (Siegel, 1983; Siegel and Glaser, 1986).

The recharge and discharge function of wetlands underlain by thick peat can be initially determined by installation of piezometers or pressure transducers in the peat and underlying mineral soil (Chason and Siegel, 1986; Boelter, 1972). The hydraulic mechanisms for the recharge-discharge areas determined in this fashion may then be determined through the hydrogeologic systems approach, usually by using numerical models to test hypotheses on the hydrologic boundaries and material properties of the porous media.

CASE STUDIES

Function reversals

The recharge function of raised bogs can be reversed seasonally to the discharge function because of water-table changes in intermediate and regional flow systems. A striking example of such a reversal was identified in the Lost River Peatland of Northern Minnesota. This large mire consists of raised bogs with diameters greater than 1 km surrounded by fens of equal size. Peat ranged from 2 to 3 m deep except on beach ridges of Pleistocene Glacial Lake Agassiz, which crossed the topographically flat peatlands at irregular intervals (Siegel, 1981).

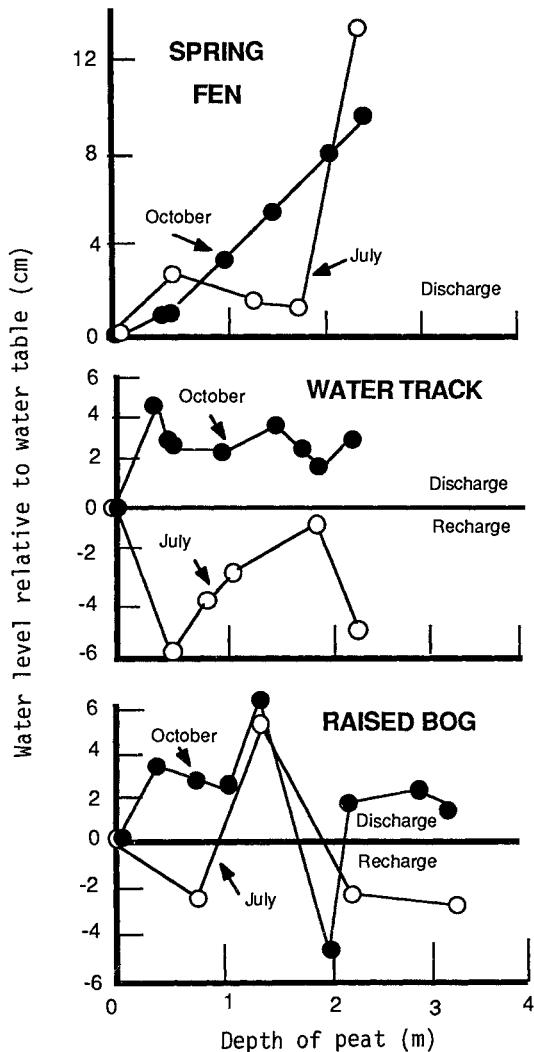
Ground-water discharge in the Lost River peatland is focused at a peat mound, previously a raised bog, where the vegetation is now that of a spring fen. Concentrations of dissolved solutes in surface-water channels in this fen are similar to that of ground water in the underlying mineral soils (Siegel and Glaser, 1986). Water levels in piezometers are above the water-table, indicating that the site is a discharge area for ground water (Figure 6.1). A larger adjacent raised bog and fen are also seasonally discharge areas (Figure 6.1).

Although the surface waters on the raised bog are characteristic of ombrotrophy (pH less than 4.2 and concentrations of calcium less than 2 mg/l), the pore water at only 0.5 m depth at the raised bog and adjacent water track is characteristic of typical ground-water found in mineral soils (pH greater than 7.0 and concentrations of calcium greater than 50 mg/l). The increase in pH, and concentrations of major metals and alkalinity with depth, further documents that ground water is being advected towards the surface of all three vegetational features (Siegel and Glaser, 1986).

The hydrologic mechanism causing both the continuous discharge of ground water at the spring fen and the reversals in recharge and discharge in the nearby fen and large raised bog are incompletely known. Computer simulations of ground-water flow suggest that the peat under the spring-fen raised bog complex could be underlain by a permeable lens of sand and gravel bounded by a topographic rise in the buried bedrock (Boldt, 1986; Siegel, 1981). The three-dimensional computer simulations of ground-water flow indicate that the spring-fen and raised bog complex may be located over the discharge zone of an intermediate scale ground-water system recharged at a beach ridge about 12 km to the north (Figure 6.2). The simulations also show that a 1 m

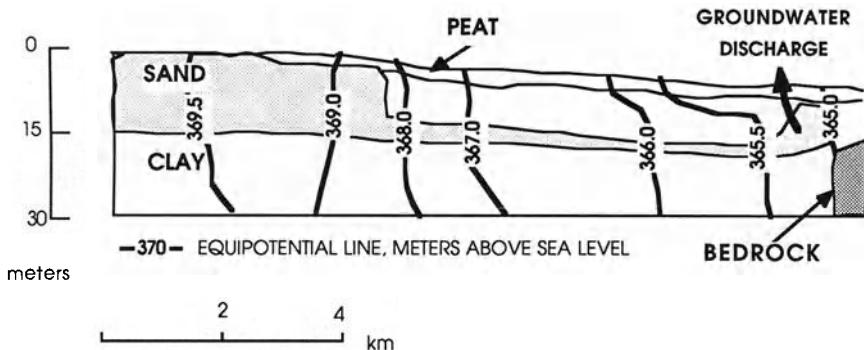
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Figure 6.1: Water level measurements in piezometer nests at the Lost River Peatland, northern Minnesota



Source: After Siegel and Glaser (1986)

Figure 6.2: North-south, numerical cross-sectional simulation through the spring fen, Lost River Peatlands



Source: After Boldt (1986)

rise in the water table on the beach ridge could cause the observed reversals of discharge and recharge in the fen and bog (Boldt, 1986).

Although this hypothesis needs to be tested by additional field studies, similar discharge of ground water to raised peat mounds has been identified elsewhere (Wilcox, Shedlock and Hendrickson, 1986; Nicols, 1983).

Regional functional analysis

Measurements of hydraulic head from wetlands in the Mendenhall Valley, south eastern Alaska give a preliminary evaluation of the recharge-discharge function. Forty-three measurements of pore water pressure were made using a specially designed probe equipped with a pressure transducer (Bennett, Siegel, Jones and Veeger, 1987). Water levels were also measured in piezometer nests (groups of monitoring wells placed at different depths in the flow system) installed in representative wetland types.

The Mendenhall Valley is underlain by glacial outwash and moraines deposited during advances of the Mendenhall Glacier. Although much of the valley has only been exposed by ice retreat during the last few hundred years (Miller, 1975), wetlands located along the sides of the valley are thousands of years old and contain peat over 1 m thick. The regional configuration of the water-table shows that ground-water generally moves from north to south and that the major streams, Mendenhall River and Montana Creek, are discharge areas (Barnwell and Boning, 1968).

A wide range of wetlands may be distinguished in the Mendenhall Valley on the basis of their topographic setting as well as their vegetation assemblages. Moss-lichen wetlands (ombrotrophic blanket bogs) occur on the upper slopes of the valley, particularly above Montana Creek, a tributary to Mendenhall River. At the head of the valley, small kettle lakes dot the recessional

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moraines of the Mendenhall Glacier. On the main valley floor, a large patterned fen has spread over the gently sloping outwash plain. Further downslope, freshwater wetlands grade into tidal marsh along the Gastineau Channel.

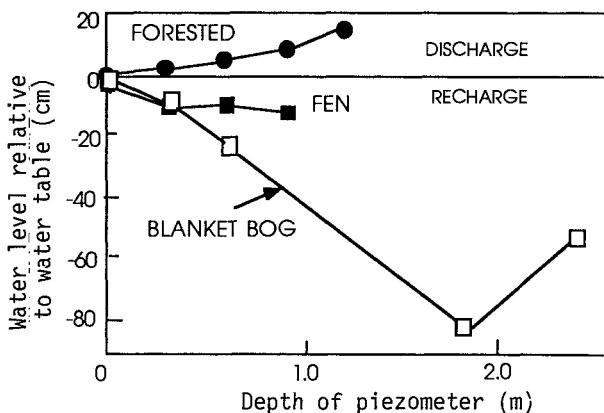
At upland blanket bogs, water levels in the piezometers are below the water table (Figure 6.3). This indicates that these wetlands are located in ground-water recharge areas. However, surface water collected in May 1986 from a linear depression on one blanket bog had a pH of 5.5 and calcium concentration of 6 mg/l, indicating a significant component of ground-water discharge of horizontal piping from the adjacent mineral soil uplands (Siegel, 1983). The emergence of fen vegetation in the linear depressions, probably the result of piping of ground-water flow in the peat, shows that a component of ground-water locally discharges to the bog surface.

Water-level measurements in the shrub-scrub wetland (fen) also showed recharge (Figure 6.3). Where peat is thick and covers large areas, fen vegetation indicates ground-water discharge (Boelter and Verry, 1977). In the Mendenhall fen, however, peat is only 0.2 m thick, and fen vegetation can obtain nutrients directly from ground-water in the mineral soil.

Ground-water discharge was determined at a forested wetland (Figure 6.3), even though its physiographic position on a mountain slope above the valley suggests a strong recharge function.

Preliminary pore-pressure measurements showed that kettle lakes in the moraines across the valley had both recharge and discharge functions, similar to those theoretically predicted by Winter (1976). The pore-water pressure probe also identified

Figure 6.3: Water-level measurements in piezometer nests showing recharge in Mendenhall Valley wetlands, Alaska in July 1986



probable areas of stream losses and gains by ground-water recharge and discharge. Water levels and ground-water quality will be monitored in the study until freeze-up to determine if these preliminary results document the dominant recharge-discharge functions or whether the direction of ground-water flow is seasonally variable. Computer modeling experiments are also being performed to simulate the observed vertical gradients in potentiometric head. Field measurements will provide data for the models on hydraulic conductivity of peat and underlying mineral soils.

DISCUSSION AND CONCLUSIONS

Field measurements indicate that it is often difficult to predict recharge and discharge from the physiographic setting of a wetland site. Even in flat mires areas, it is uncertain that raised bogs always are recharged areas for local ground-water flow. Although it seems intuitive that wetlands connected to major lakes and streams should be ground-water discharge areas, reversals of head can and do occur as transient local ground-water mounds develop along nearshore areas.

Current classifications of wetlands are inadequate to address the recharge-discharge function of wetlands. Classifications largely based on vegetation communities and type of substrate (i.e. Cowardin, Carter, Golet and LaRoe, 1979) are not useful for evaluating ground-water-wetland interaction except where vegetation is very sensitive to water chemistry, such as in northern mires.

Classifications based predominantly on hydrologic considerations (Novitski, 1982) do not adequately evaluate the recharge-discharge relationship of wetlands because they center on the local physiographic position of the wetland rather than on the position of the wetland in relation to the larger hydrogeologic system. The important interaction of ground-water flow systems at different scales is not considered.

It is imperative that some instrumentation be used in evaluating the recharge-discharge function of wetlands. At a minimum, potentiometric head should be determined from piezometers placed in the organic and upper mineral soil in the wetland. Installation of such instrumentation is inexpensive and simple. It will qualitatively determine if the piezometer site is a recharge or discharge zone at the time of sampling. Alternative approaches require using a pore-water pressure probe or measuring selected chemical constituents if there is a significant contrast between the water chemistry in the peat and the underlying mineral soil.

The recharge-discharge function of wetlands is so site specific that generalizations with respect to physiographic setting cannot yet be made without a larger data base of detailed case studies. Future studies should combine both field and numerical simulation methods to best evaluate observed variability in the recharge-discharge function of wetland systems.

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Chapter Seven

SOME COMMENTS ON THE RELATION BETWEEN GROUND WATER AND WETLANDS

Virginia Carter and Richard P. Novitzki

INTRODUCTION

One frequently stated myth used as a justification for wetland preservation is that 'wetlands are ground water recharge areas'. This statement is true for some wetlands but invalid for many others. Actually, the relation between ground water and wetlands can be exceedingly complex. Recharge and discharge are natural processes that occur throughout the landscape (Sather and Stuber, 1984; Carter, 1986). The magnitude and timing of these processes depend upon such variables as the interrelation between local, intermediate and regional ground-water flow systems, position of local water table, geologic setting, ratio of vertical to horizontal hydraulic conductivity in the basin, depth and width of the basin, local slope and relief, and location of ground-water divides.

Calculation of hydrologic and nutrient budgets for wetlands requires serious consideration of ground-water inputs and outputs (Winter, 1978b; LaBaugh, 1986). These inputs and outputs are critical to the existence and maintenance of wetlands, and it is desirable to understand and quantify them because of their importance to water chemistry, water supply, aquifer replenishment and wetland function (Sather and Stuber, 1984). Until recently, there have been relatively few studies made of the relation between ground water and wetlands. In this paper, we briefly summarize the theoretical aspects of recharge and discharge as related to lakes and wetlands and present the results of several recent studies that shed light upon the complex relation between ground water and wetlands. We have not attempted to search out all such studies; those discussed herein are part of ongoing research by us or by our colleagues in the US Geological Survey.

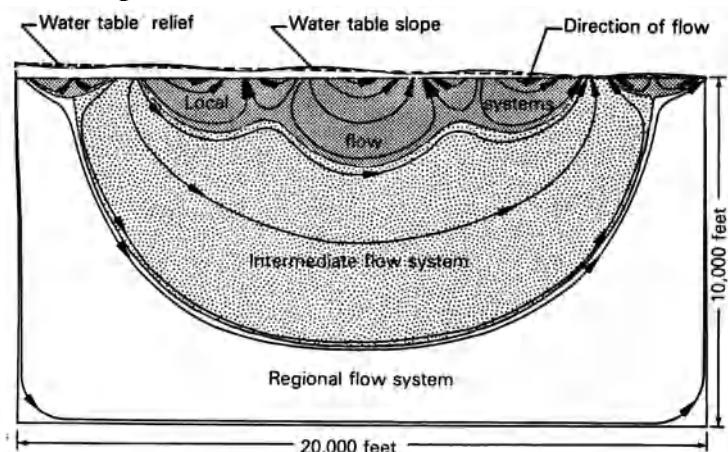
THEORETICAL ASPECTS

Theoretical analyses of ground-water flow patterns under varying hydrogeologic conditions preceded actual field studies of the interaction of ground water with lakes and wetlands (Toth, 1963; Meyboom 1966a; Freeze and Witherspoon, 1966, 1967, 1968; Winter, 1976, 1978b,c,1981). Toth (1963) theorized three types or scales of ground-water flow occurring in small basins; local, intermediate

and regional (Figure 7.1; Winter, 1976). A local system of ground-water flow has its recharge area at a topographic high and its discharge area at an adjacent topographic low. An intermediate system has one or more topographic highs and lows located between the recharge and discharge areas. A flow system can be considered regional if its recharge area occupies the water divide and its discharge area lies at the bottom of the basin. Water levels in local systems at shallow depths are most effected by seasonal recharge and discharge. Different recharge areas and flow path lengths contribute to differences in the chemical composition of water in different systems. Toth (1963) also suggested that:

1. A regional flow system will develop in a basin where there is negligible relief and a general slope; recharge occurs between the drainage divide and the midline and discharge between the midline and the valley bottom. Decreasing velocity and longer flow paths of water at depth in a regional system increase contact time and may result in a gradual increase in dissolved minerals.
2. With well-developed relief, local flow systems originate with boundaries between adjacent systems located at highest and lowest elevations. Local systems may cause alternating recharge and discharge areas across a valley and, because the origin of water obtained from closely juxtaposed locations may not be the same, abrupt changes in water chemistry may occur.
3. At subsurface points where flow systems meet, an area of stagnant ground-water is formed.
4. Ground-water movement is retarded under extended flat areas and discharge is by evapotranspiration (ET). These areas may have high concentrations of soluble salts.

Figure 7.1: Local, intermediate and regional systems of ground-water flow



Source: After Toth (1963); modified by Winter (1976)

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Winter (1976) used a two-dimensional numerical model of the detailed patterns of ground-water seepage to and from lakes in a wide variety of hypothetical hydrogeologic settings. His findings may also be applied to many wetlands including the shallow (<2 m) ponds or lake margins defined as wetland by Cowardin, Carter, Golet and LaRoe (1979). His studies showed:

1. Interactions between lake and ground water are controlled by the position, extent and hydraulic conductivity of all the geologic units in the ground-water system.
2. These interactions are dependent on the height of the water table divide on all sides of the lake relative to lake level and depth.

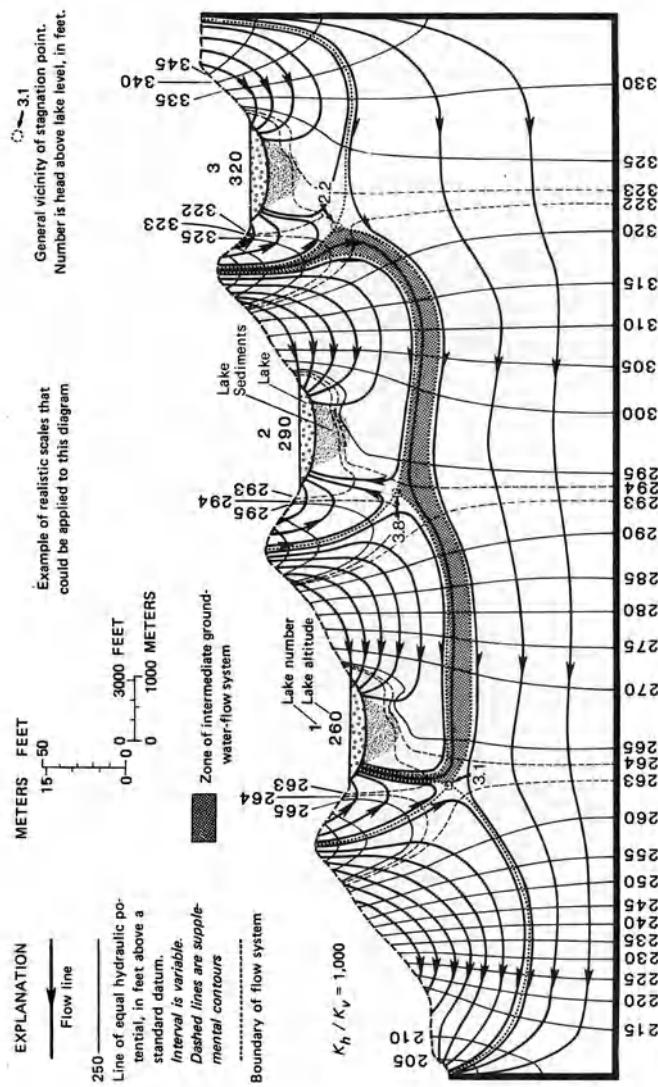
More specifically, his work shows that the movement of ground-water to (discharge) or from (recharge) a lake depends on the continuity of the boundary separating the local ground-water flow system associated with the lake from the intermediate and regional flow systems passing at depth below the lake. The key to determining this continuity and whether there is recharge from, or discharge to, the lake is the presence and location of the point of minimum hydraulic head along the boundary - the stagnation point (Figure 7.2). If, as shown, the head at this point is higher than that of the lake, water cannot move downward from the lake. Winter (1978c) concluded that several conditions could cause outflow from a lake to the surrounding ground-water system including lowering the water table, especially in the downslope side of the lake, increasing the ratio of horizontal to vertical permeability of the basin, increasing the hydraulic conductivity of or raising the elevation of aquifers in the ground-water basin, or increasing the depth of the lake. In 1981, he showed that the water table gradient between the lake and the regional discharge area also affected recharge or discharge from a lake. When several lakes occurring at different elevations are simulated, each lake and its local flow system acts as an independent entity with outseepage (recharge) from a lake entering the regional ground-water flow system. Most ground-water flow into a lake occurs in the littoral zone and most loss occurs through the low permeability sediments at depth (Winter, 1978b). However, if there is no water-table mound on the downslope side of a lake, recharge may occur through the littoral zone. Finally, Winter (1981) pointed out that a concave-up break in water-table slope may affect seepage through a nearby lake, but also results in a ground-water discharge area (wetland) on the lower slope segment next to the break in slope (Figure 7.3).

FIELD STUDIES

Indiana Dunes National Lakeshore

Shedlock, Wilcox and Thompson (1986) and Wilcox, Shedlock and Hendrickson (1986) have studied the hydrology and hydrochemistry of the southern shore of Lake Michigan with special emphasis on the interaction between ground water and a large interdunal wetland known as Great Marsh (Figure 7.4). The National Lakeshore lies in the Calumet Lacustrine Plain, which has high relief charac-

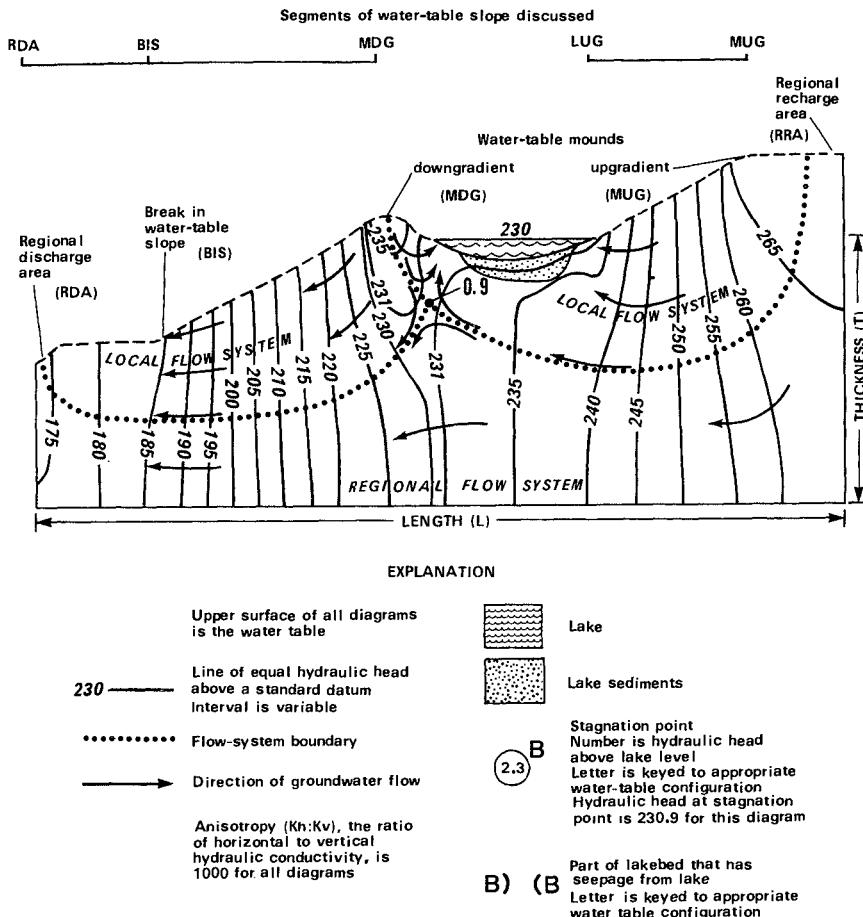
Figure 7.2: A quasi-quantitative flow net of ground-water flow near lakes in a multiple-lake system. Shallow, deep and intermediate flow systems and stagnation points are shown.



Source: From Winter (1976)

HYDROLOGIC & WATER QUALITY VALUES OF WETLANDS

Figure 7.3: Distribution of hydraulic head, ground-water-flow directions, and ground-water interaction with a lake associated with a water-table slope that has a break in slope nearby. Note ground-water discharge associated with break in slope



Source: From Winter (1981)

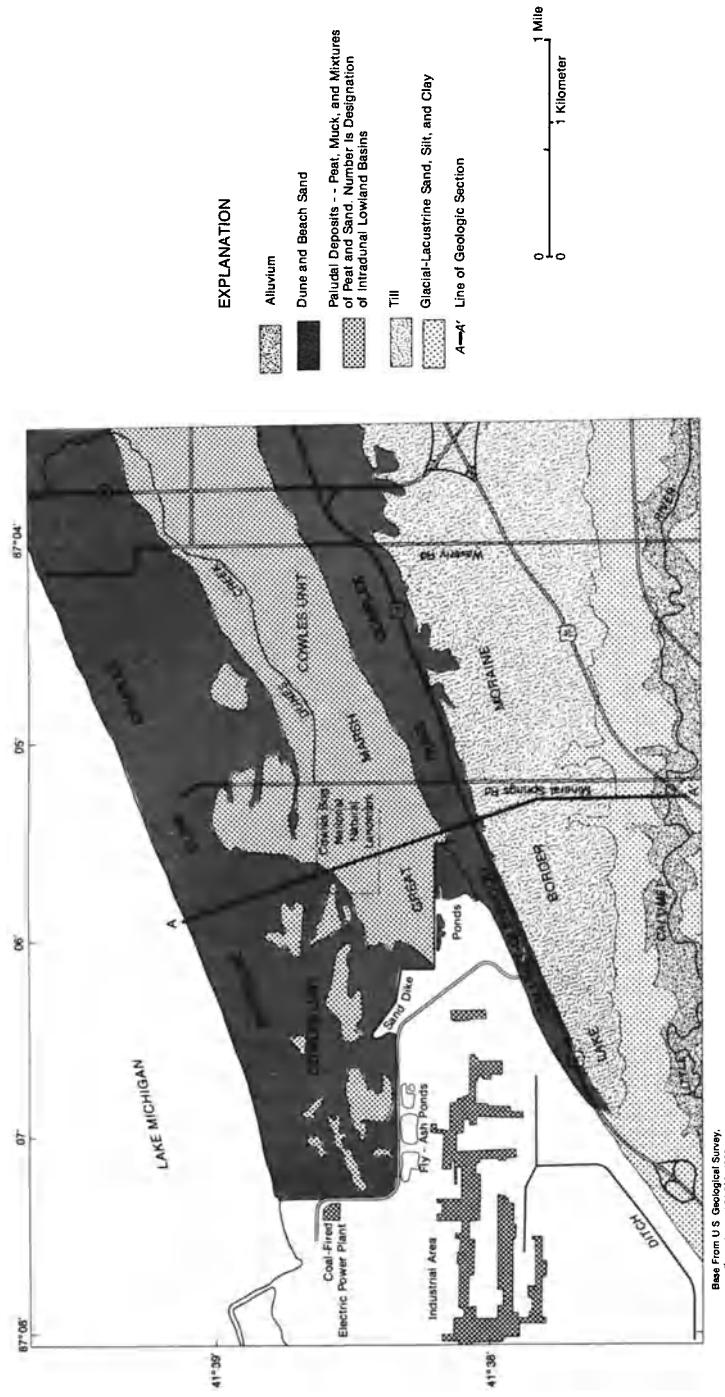
terized by sand dunes and interdunal wetlands. The Great Marsh is bordered on the south by the Lake Border moraine and on the north by Lake Michigan and the adjacent dune complex (Figure 7.4). This marsh contains a 56-acre tract with a raised peat mound called Cowles Bog. Previous hydrologic and modeling studies of the geometrically complex system of aquifers underlying the study area were done by Marie (1976), Meyer and Tucci (1979) and Gillies and Lapham (1980). Insufficient local stratigraphic information led Gillies and Lapham (1980) to state the need for more detailed hydrogeologic information.

Numerous test holes, piezometers, and observation wells installed from 1979 and 1984 have provided information on the vertical distribution of aquifers beneath Great Marsh. Ground-water levels and chemical analyses of numerous water samples from these wells guided the present interpretation of the hydrologic system. In addition to the surficial aquifer of sand, peat, and mud that supports a variety of wetland and dune vegetation, sand layers below the buried till sheet of the Lake Border moraine form a confined aquifer under the study area (Figure 7.5) called the subtilt aquifer.

Regional, intermediate and local flow patterns, as described by Toth (1963) and Winter (1976) have been recognized in the glacial drift and upper bedrock-aquifer system in the study area. The regional flow system originates at a major end moraine south of the study area and discharges into the base of the glacial drift aquifer system near Lake Michigan. The Lake Border moraine creates a ground-water divide in the glacial drift and an intermediate flow system in the subtilt aquifer. Nearly all the discharge from the intermediate flow system is by upward leakage through the till sheet into Great Marsh because the subtilt aquifer pinches out at the northern edge of Great Marsh (Figure 7.5). At Cowles Bog, a breach in the till sheet allows water to flow directly from the subtilt aquifer into the overlying marl, sand and peat. This discharge has led to the growth of a raised peat mound with a high water-table and a local pattern of radial outflow from the mound (Figure 7.6). Stagnation zones probably exist west of the peat mound and at the convergence of the intermediate and regional flow cells in the subtilt aquifer below the Lake Border moraine. The local flow systems in the dunes that border the Great Marsh cause shallow ground water from the dunes to flow toward the marsh. The convergence of these different flow systems in the Great Marsh leads to abrupt changes in the chemistry of both wetland ground and surface water.

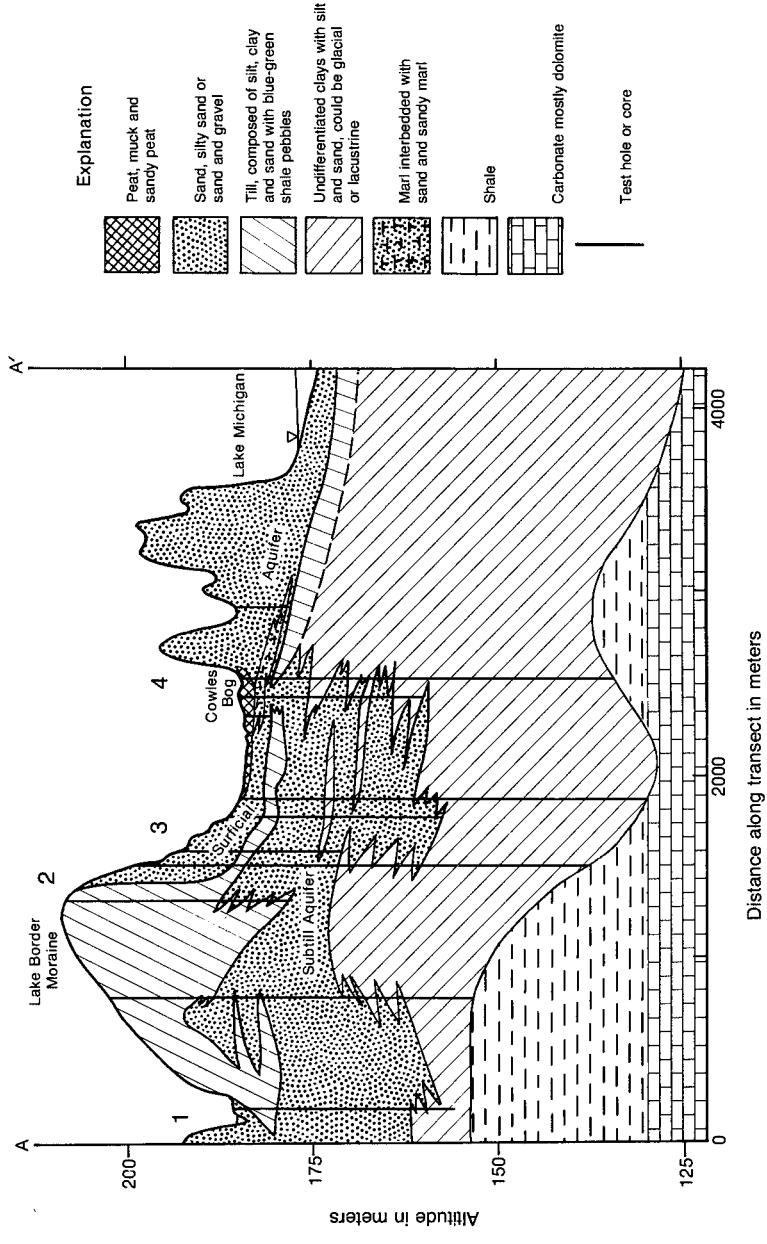
The authors show that, for this hydrogeologic setting, the direction of vertical flow between the surficial aquifer (wetland) and the underlying confined aquifers is related to changes in water-table elevation as a function of topography, and to the areal extent of the confined aquifers and their hydraulic connections to upland recharge areas. They also conclude that there are both recharge and discharge zones in the Great Marsh. Interaction of wetlands with ground-water is not necessarily uniform over a wetland or within a wetland-upland complex, and an interdisciplinary approach involving biology, hydrology, geology, and chemistry

Figure 7.4: Map of study area showing surficial geology, drainage, and location of Cowles Bog



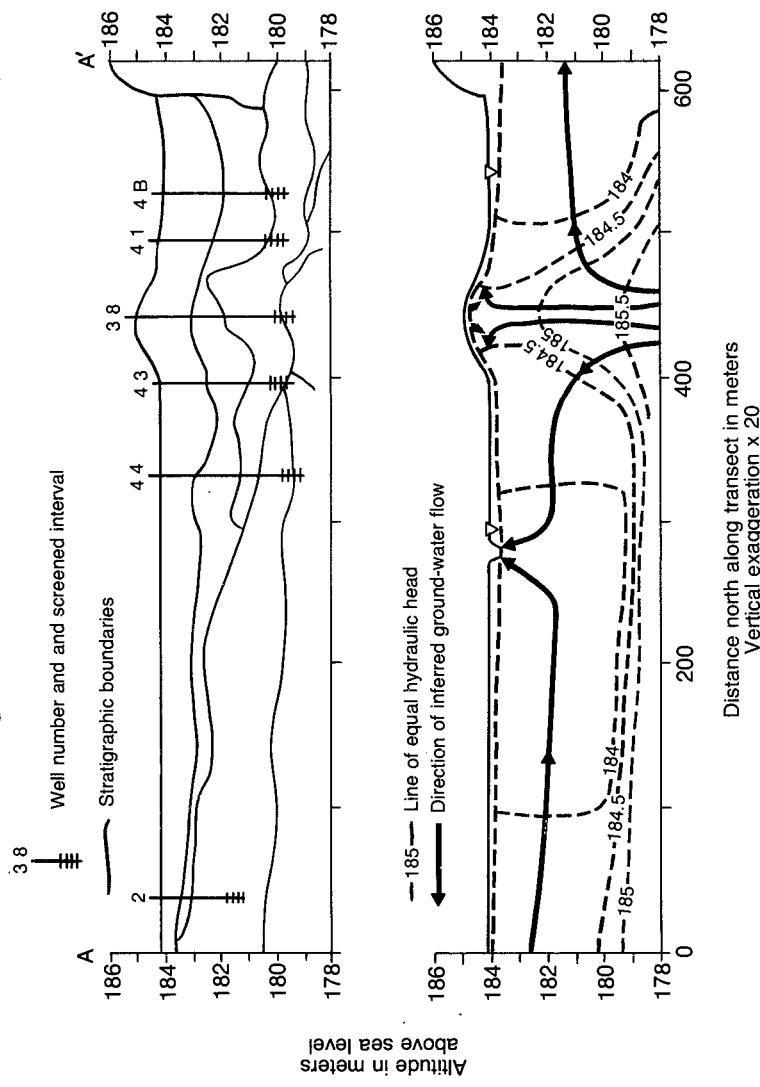
Source: From Shedlock et al. (1986)

Figure 7.5: Geologic section through Cowles Bog



Source: Shadlock et al. (1986)

Figure 7.6: Hydrogeologic cross section of Cowles Bog Wetland perpendicular to the long dimension of the basin (N-S) showing well locations, contours of hydraulic head, and groundwater flow paths



Source: From Wilcox et al. (1986)

was needed to interpret the complex hydrology and chemistry of this wetland complex.

Prairie wetlands in North Dakota

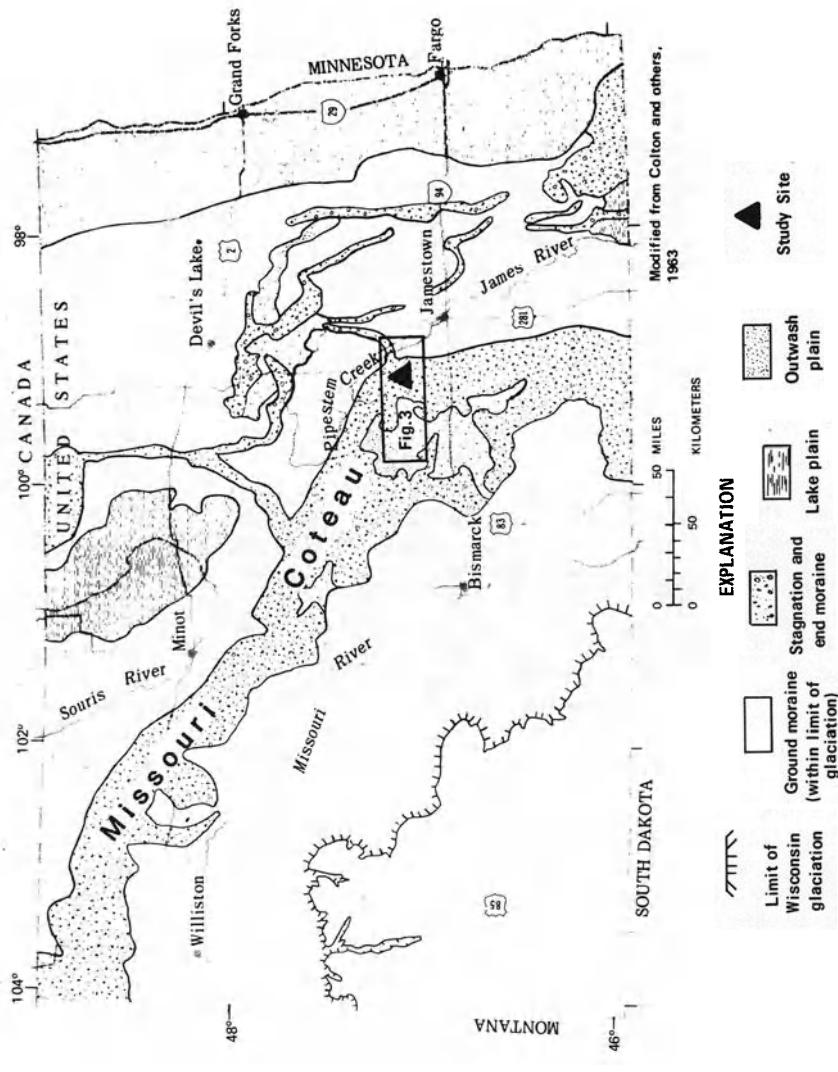
Between 1979 and 1982, Winter and Carr (1980) and LaBaugh, Winter, Adomaitis and Swanson (1986) studied the relationship of hydrologic setting and temporal variability in hydrology to the geochemical characteristics of a group of prairie wetlands in the Cottonwood Lake area of North Dakota. The study site is located in a regional topographic high near the eastern edge of the Missouri Coteau, and is underlain by more than 130 m of glacial drift - largely clayey, silty till with a few lenses of sand (Figure 7.7). Local relief in the study site is about 30 m. Three wetlands in the highest part of the area are separated from eight wetlands at an intermediate level by a steep, 15 m high slope. Three other wetlands are located on the valley floor. A network of water-table wells and a nest of five shallow piezometers were used to determine the recharge-discharge relation in the wetlands and the water-table configuration in the study site. Numerical simulations were used to conceptualize the regional and local flow systems (Winter and Carr, 1980). Four wetlands - two temporary (T8 and T3) and two permanent (P1 and P8) - were selected for the detailed study reported by LaBaugh *et al.* (1986) (Figure 7.8). Chemical analyses of wetlands and ground water were correlated with hydrologic regime.

The study showed that there is great variability in the mechanisms that control direction of water flow between the ground-water system and the wetlands. Quantity of rain or snow and timing of snowmelt and rainfall changed water flow seasonally and annually. Wetland T8, at the highest location, recharged ground water, the other temporary wetland, T3, received ground-water input and lost water to the ground-water system. Both permanent wetlands received ground-water discharge. Reversals of flow occurred occasionally between two of the wetlands. The ground-water level data also showed that high points in the water-table did not always occur beneath the land-surface highs. Winter (US Geological Survey, personal communication, 1985) has postulated the occurrence of water-table mounds adjacent to wetlands immediately after heavy precipitation events. These mounds may result, at least temporarily, in higher water tables near the edge and lower water tables in the center of topographic highs. In addition to these hydrologic findings, there were significant differences in the chemical composition of these neighboring wetlands based upon their hydrologic regimes.

Great Dismal Swamp

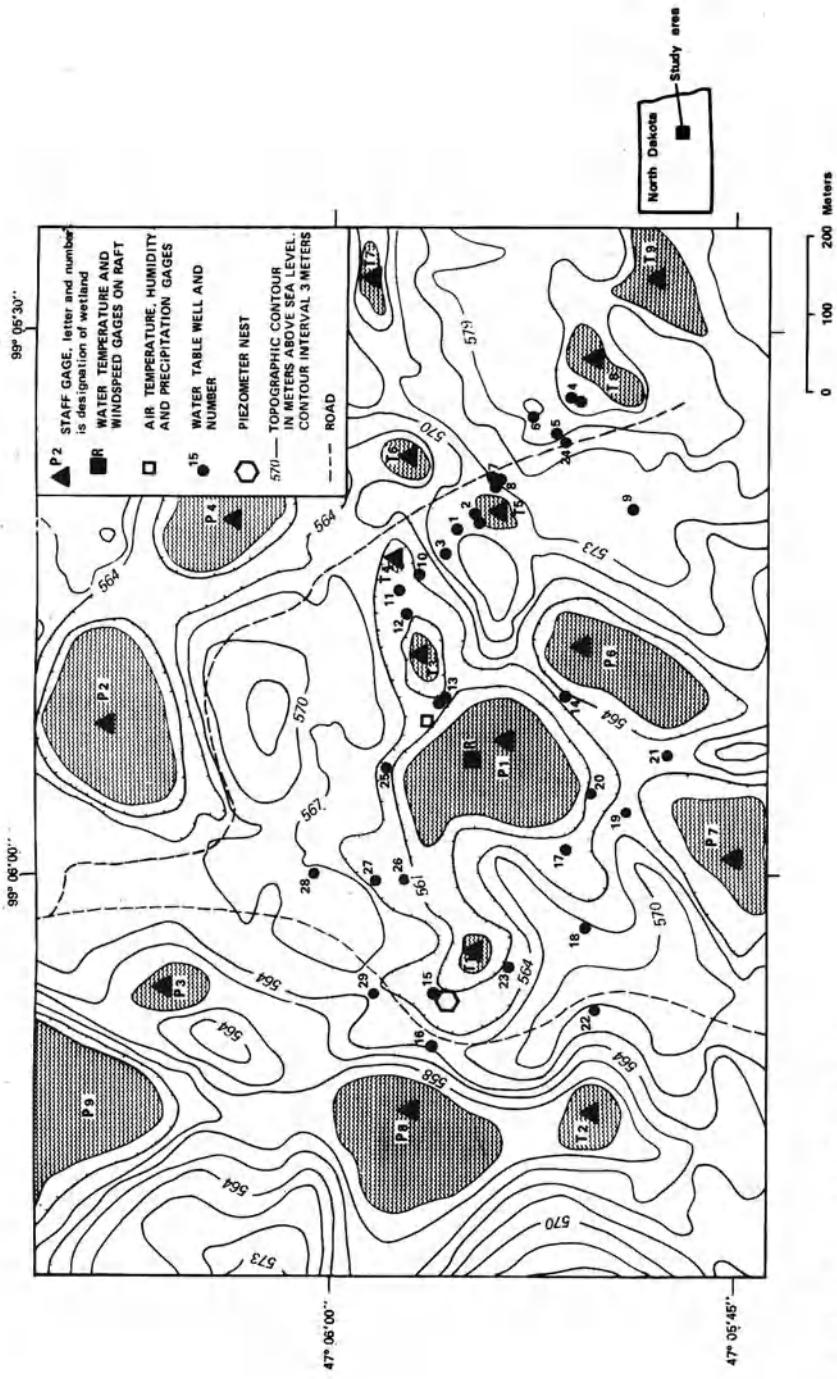
Since 1979, Carter (US Geological Survey, unpublished data) has conducted a study of the hydrology, soils and vegetation on the western upland-to-wetland transition zone of the Great Dismal Swamp of Virginia and North Carolina (Figure 7.9). Description of the ground-water movement in the transition zone and clarification of the relation of ground-water movement to geologic control appears to be the key to unraveling the complex interaction of geology, hydrology, and ecology of this zone.

Figure 7.7: Glacial geology of North Dakota and location of study site in the Cottonwood Lake area,



Source: Winter and Carr (1980)

Figure 7.8: Location of hydrologic instrumentation at the study site



Source: Winter and Carr (1980)

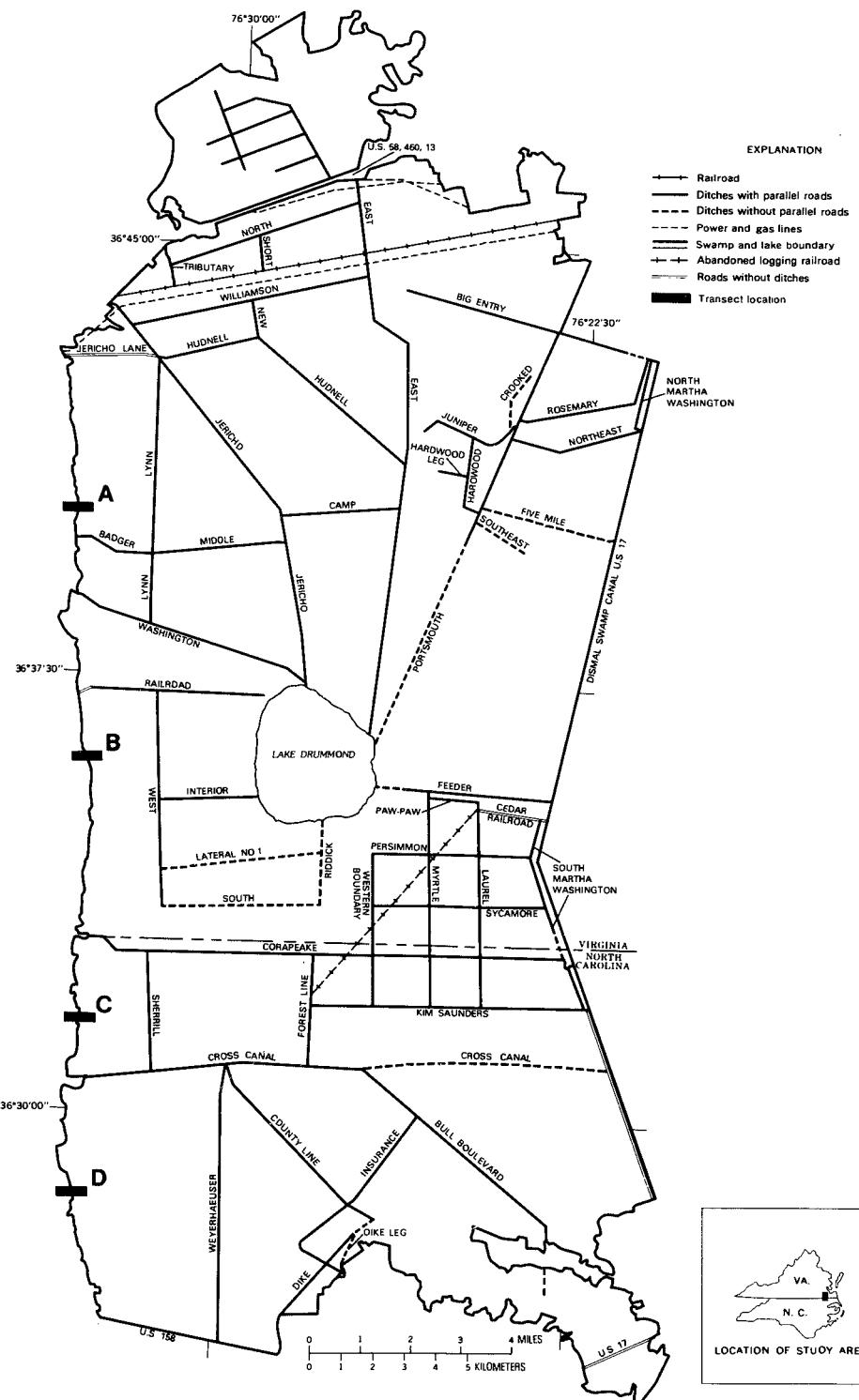


Figure 7.9: Map showing location of Great Dismal Swamp

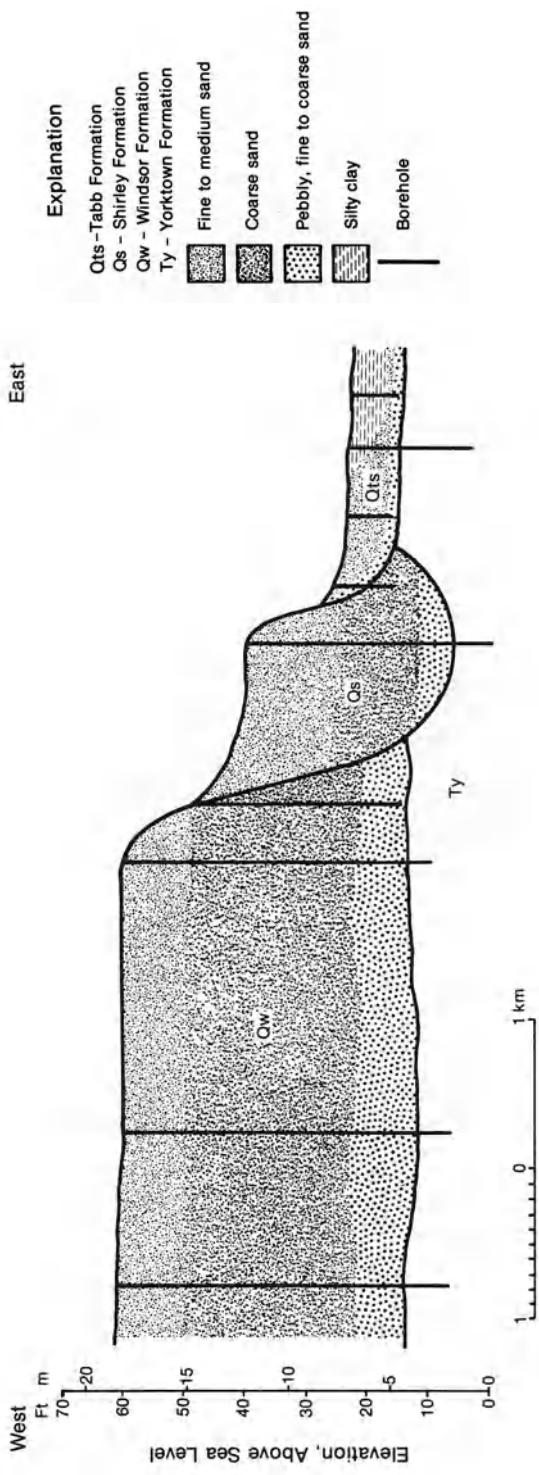
On the western edge of the Great Dismal Swamp, the Suffolk Scarp - a Pleistocene shoreline feature - rises abruptly to an elevation of 18 to 21 m above sea level. The main part of the swamp, 84,000 ha in area, slopes gently eastward at about 0.2 m per km from an elevation of 7.6 m near the toe of the Suffolk Scarp. The western transition zone is a 48 km-long, 400 - 630 m-wide zone of variable slope lying on the eastern flank of the Scarp between the agricultural fields along the crest and the interior of the swamp to the east. Four east-to-west transects - two in North Carolina and two in Virginia - cross the transition zone from wetland to upland, incorporating the elevation range from 6 to 11m. Water-table wells and piezometers installed along these transects provided the hydrologic information for this report.

Recently, Peebles, Johnson and Berquist (1984) and Peebles (1984) have revised the surficial lithostratigraphy of the coastal plain in the vicinity of the Great Dismal Swamp. Peebles (1984) has also developed a depositional model accounting for the coarse basal fining-upward sequences that accumulate during a marine transgression across a dissected coastal plain. The Great Dismal Swamp is underlain by the Tabb Formation of late Pleistocene age, and the abutting Suffolk Scarp is middle Pleistocene Shirley Formation or (to the south) Windsor Formation (Figure 7.10). These three formations are underlain by the impermeable Yorktown Formation of early Pliocene age. The movement of water eastward or upward within the permeable basal sand facies of the Tabb Formation (Tabb aquifer) is restricted by a less-permeable facies to the east, and a less-permeable, fine-grained layer of soil above thus creating artesian head in the Tabb aquifer (Lichtler and Walker, 1974). At three of four core-transect locations along the swamp margin, the Tabb aquifer abuts a coarse basal sand and gravel layer at the base of the Shirley or Windsor Formation to the west, providing a good hydraulic connection to the large recharge area of those formations (Figure 7.10). Ground-water discharges into swamp along the western margin as a result of local flow systems on the Scarp, a concave-upward break in slope near the bottom of the Scarp, and the confined head in the Tabb aquifer. At the fourth and northernmost transect, the Tabb aquifer lies below and is not directly connected to the coarse basal facies of the Shirley Formation; as a result, seepage occurs along the edge of the swamp. Water levels at this transect are consistently high compared with those at the other transects. Wells developed in the Yorktown or below are artesian, suggesting that a stagnation point may exist between the local and regional flow system that prevents the downward leakage of water from the swamp and accounts for its persistence despite attempts to drain it.

New York watersheds

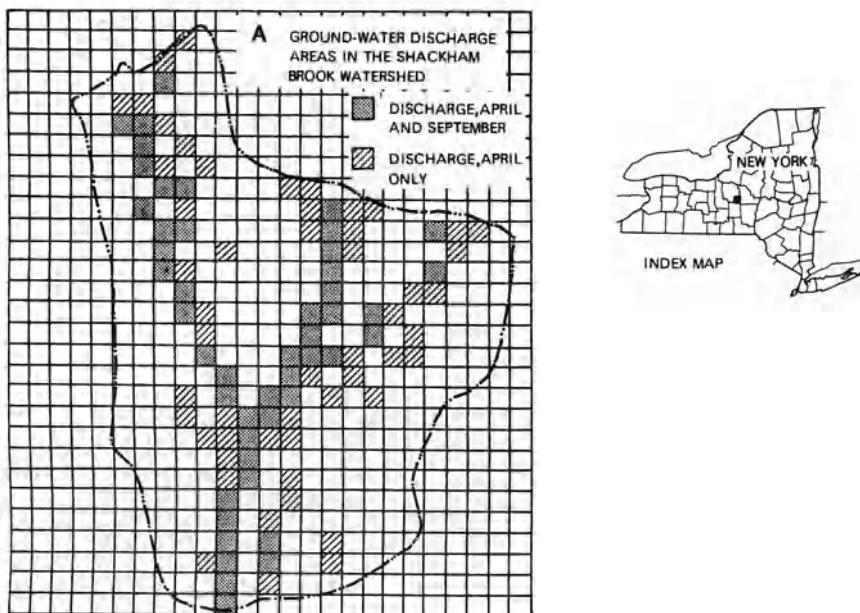
Since 1982, Lyford and others (US Geological Survey, unpublished data) have conducted a Regional Aquifer System Analysis study to describe ground-water conditions in the surficial unconsolidated aquifers of the northeastern United States. As part of the study they have developed ground-water flow models of selected aquifer

Figure 7.10: Section showing relationship of Tabb Formation (Qts) to Shirley Formation (Qs) and Windsor Formation (Qw) to the west



Source: From Peebles (1984)

Figure 7.11: Ground-water discharge areas (A) and wetlands (B) in the Shackham Brook watershed, New York

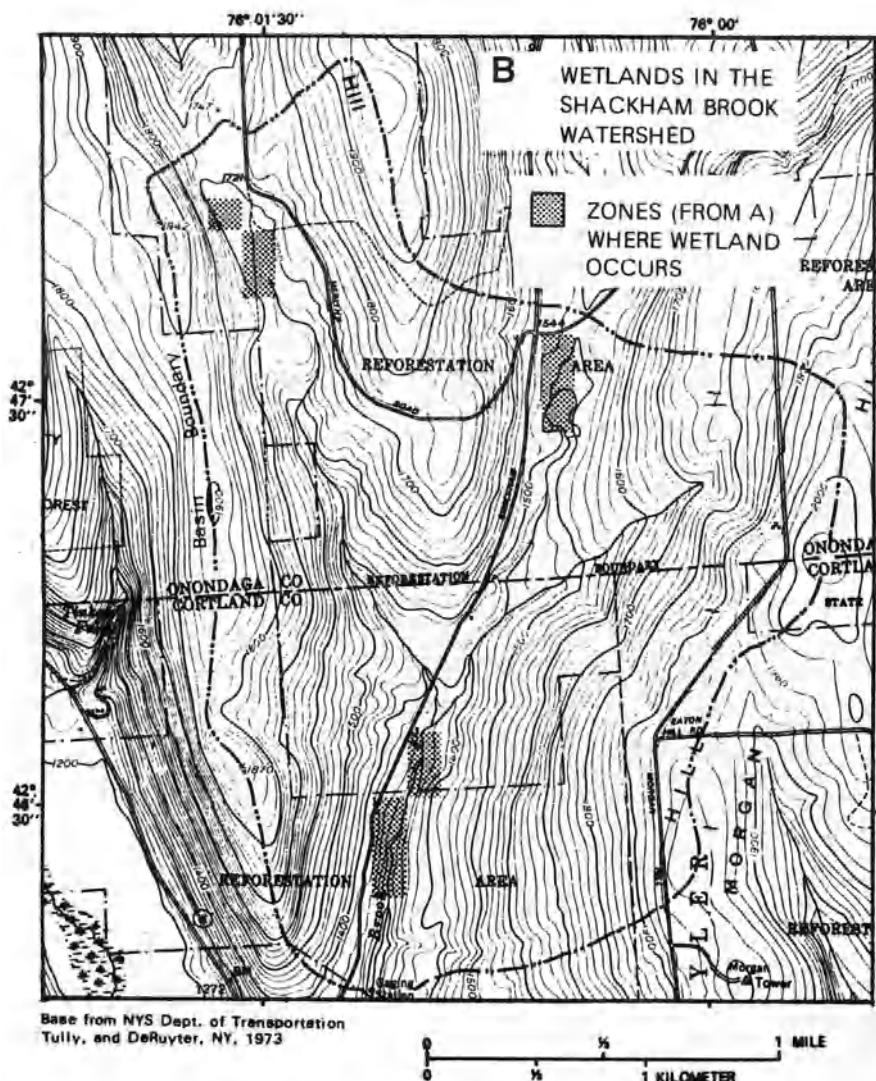


units. One result of this modeling effort (F.P. Lyford, US Geological Survey, written communication, 1986) was identification of zones where ground-water discharges to the land surface during periods of both high and low ground-water levels (April and September, respectively). Zones where ground-water discharges to the land surface in a small watershed in central New York are shown in Figure 7.11. Superimposing on this map the locations of wetlands in this watershed (Figure 7.11) mapped by the New York State Department of Environmental Conservation (C.R. Vass, New York State Department of Environmental Conservation, written communication, 1986) reveals that wetlands occur only where ground-water discharges to the land surface. Novitzki (1979, p. 18; 1982, p. 5) also suggested that wetlands in Wisconsin were usually in contact with aquifers.

DISCUSSION

These examples illustrate the complexity of recharge-discharge relationships in wetlands and the impossibility of designating all wetlands either discharge or recharge areas. Many wetlands lie in depressions and receive ground-water discharge from local, intermediate, or regional flow systems. Wetlands may also develop where they receive ground-water discharge on slopes (e.g. the Great Dismal Swamp), or where seepage facies occur because of peculiarities within the local ground-water system. Some depression

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wetlands such as the T8 of LaBaugh et al. (1986) may be perched above the local water table and may recharge the local system - a type of recharge referred to by Lissey (1971) as depression-focused. It appears evident that further research will be needed before this particular wetland function can be evaluated accurately and efficiently, but current research suggests that many more wetlands are ground-water discharge areas than recharge areas. Perhaps recharge and discharge should both be considered valuable functions of wetlands and this particular functional value in proposed ranking and evaluation methodologies should be reassessed.

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Chapter Eight

WATER QUALITY FUNCTIONS OF WETLANDS: NATURAL AND MANAGED SYSTEMS

Robert K.Bastian and Jay Benforado

INTRODUCTION

Freshwater, brackish and saltwater wetlands have inadvertently served as natural water treatment systems for centuries. Because of their transitional position in the landscape between terrestrial and aquatic ecosystems, some wetlands have been subjected to wastewater discharges from both municipal and industrial sources. Wetlands have also received agricultural and surface mine runoff, irrigation return flows, urban stormwater discharges, and other sources of water pollution. It is only in the past few decades, however, that the planned use of wetlands for meeting wastewater treatment and other water quality objectives has been studied and implemented. The functional role of wetlands in water quality improvements has been identified as a compelling argument for wetland preservation (Horowitz, 1978), and in some cases, for creation. Odum (1978) noted that 'Numerous patches and strips of wetlands ... act as buffers and filters between man's urban and agricultural development and his most vital natural resource - water.'

MECHANISMS THAT AFFECT WATER QUALITY IN WETLANDS SYSTEMS

Water quality improvement has been observed in many types of natural wetlands, such as freshwater marshes, northern bogs, southern swamps, bottomland hardwood forests, brackish and saltwater marshes, and constructed wetland systems (US EPA, 1983,1985; US EPA/US DOI, 1984; Godfrey, Kaynor, Pelcsarski and Benforado, 1985). Wetland systems can often tolerate conditions associated with wastewater input, such as oxygen depletion in water and sediment, and effectively remove or transform nutrients and other wastewater contaminants. The impact of wastewater addition on wetlands is generally less than on terrestrial or aquatic communities because wetland plants are preadapted to periods of standing water and water-logged soils, as well as to reducing conditions.

Stillwater wetlands (both palustrine and lacustrine) can provide effective treatment, if the wastewater percolates through

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peat before reaching ground water or surface water. This organic filter represents a significant, albeit finite, nutrient sink. Wetlands that are adjacent to streams, lakes or rivers and are intermittently flooded can also provide treatment, although some of the nutrients and other constituents are subject to dilution in receiving waters.

Kadlec and Kadlec (1978) suggest in their review of wetlands and water quality that every water quality parameter can be altered by passage through a wetland ecosystem. The concentrations of nutrients (various forms of nitrogen, phosphorus, potassium and micronutrients), heavy metals, pesticides and other chemical constituents, organic matter, man-made organic chemicals, dissolved oxygen and other suspended solids, bacteria and other pathogens can all be affected. Wetlands appear to perform all of the biochemical transformations of wastewater constituents that take place in conventional wastewater treatment plants, in septic tanks and their drainage fields, and in other forms of land treatment (Brinson and Westall, 1983).

Wetland ecosystem properties that contribute to wastewater renovation include high plant productivity, high decomposition rates, large adsorptive areas of sediments and low oxygen content of sediment. The tendency for wetland sediments to become anaerobic enhances retention of many compounds. This, together with aerated conditions in the water column and upper sediment layer, allows many processes to occur at the same time: formation of relatively insoluble phosphorus-metal complexes and metal sulfides; and the removal or conversion of nitrogen through nitrification, denitrification, ammonification and volatilization.

Dense surface vegetation promotes uniform distribution and flow of water across the wetland. Vegetation also shades the water surface, which limit algae development typical of ponds and lakes, and the resultant suspended solids' concentrations in the outflow from the wetland. Submerged vegetation provides extensive surface area for attached biological growths, which appear to play an even more important role than plant uptake in water quality enhancement. The oxygen pump mechanism utilized by cattails, Phragmites, and similar plants in saturated soils results in aerobic microsites adjacent to the plant roots in an otherwise anaerobic root zone.

The operation and pollutant removal mechanisms in wetland systems are similar to overland flow land treatment systems. Overland flow systems utilize thin-sheet flow of wastewater down a gentle, uniformly sloping, grass-covered field (US EPA, 1984). Overland flow land treatment is currently used in the United States and other countries for achieving both secondary and advanced treatment requirements. A major difference between these systems, however, is the fact that the detention time for wastewater is usually only hours in overland flow systems vs. days for wetland systems (Reed, Bastian, Black and Khettry, 1984).

In both kinds of system the wastewater may require little treatment (e.g. primary settling) prior to application, but preapplication treatment of wastewater applied to wetland systems has varied from primary settling to greater than secondary treatment.

As with other land application systems, wetlands that are over-loaded are likely to exhibit inefficient constituent removal.

Clearly, many processes affect removal and transformation rates of nutrients and other water quality parameters, including sedimentation, adsorption onto soil particles, plant uptake and cycling, microbial decomposition, and denitrification (Tables 8.1 and 8.2). Each rate is greatly dependent upon many controlling variables such as soil type (organic vs. mineral), pH, climate, flooding regimes, vegetation type, nutrient loading rate, etc. The hydrologic regime and sediment levels in the wetland tend to be the dominant physical factors that control processes.

The range of environmental conditions across wetland types is quite diverse and probably accounts for observed differences in nutrient removal efficiencies (Table 8.3). Most wetlands have the ability to remove, and retain or transform nitrogen and phosphorus from water, but at variable rates. Suspended and particulate matter can be effectively settled or filtered out by wetland vegetation and/or soils. The heavy metal content of wastewater appears to be reduced as it passes through wetlands and at least initially appears to accumulate in the sediments and vegetation of the wetland, although no long-term studies have been conducted to determine exactly how these metals are cycled or lost. It also appears that hydrocarbons which accumulate on wetland soil or vegetation surfaces can be degraded by microbial activity (Kelly, Harwell and Giblin, 1982; Godfrey *et al.*, 1985). Removal and die-off rates of pathogens from wastewaters discharged into wetlands have been reported as very high in some places, but highly variable in others (Ewel and Odum, 1985; Gearheart, Williams, Holbrook and Ives, 1986). However, the fact that many types of bacteria, including coliforms and Salmonella spp. from wildlife, seem to thrive in wetlands only serves to complicate the many health-related issues further.

In a region-by-region review of nutrient and metal uptake functions of wetlands, Nixon and Lee (*in press*) concluded that a 'credible quantitative assessment' of the role of wetlands in water quality cannot now be done due to insufficient data. While helping develop EPA's 'Wetlands Research Plan 1985', Zedler and Kentula (1985) thoroughly reviewed both published and unpublished sources of information covering water quality and related hydrologic functions of wetlands and concluded that the water quality functions of freshwater wetlands are poorly understood:

Nutrient retention and transformation roles have been used for control actions at the state level. The ability of wetlands to reduce organic toxicant and heavy metal loadings is widely assumed. However, none of the functions has been comprehensively quantified.

Clearly, more mass-balance data and long-term studies are needed.

Table 8.1: Removal mechanisms in wetlands for the contaminants in wastewater

Mechanism	Contaminant affected ^a						Description	
	Settlerable solids	Collodial solids	BOD	Nitrogen	Phosphorus	Heavy metals	Refractory organics	Bacteria & viruses
<u>Physical</u> Sedimentation	P	S	I	I	I	I	I	Gravitational settling of solids (and contaminants) in pond/marsh settings
Filtration	S	S						Particulates filtered mechanically as water passes through substrate, root masses, or fish
Absorption		S						Interparticle attractive force (van der Waals force)
<u>Chemical</u> Precipitation				P	P	P	P	Formation of or co-precipitation with insoluble compounds
Absorption				P	P	P	P	Adsorption on substrate and plant surfaces
Decomposition				P	P	P	P	Decomposition or alteration of less stable compounds by phenomena such as UV irradiation, oxidation, and reduction

Table 8.1 (continued)

<u>Biological</u>						
Bacterial metabolism ^b	P	P	P	P	P	P
	Removal of colloidal solids and soluble organics by suspended, benthic, and plant-supported bacteria. Bacterial nitrification/denitrification					
Plant metabolism ^b	S	S				
	Uptake and metabolism of organics by plants. Root excretions may be toxic to organisms of enteric origin					
Plant absorption	S	S	S	S	S	S
	Under proper conditions significant quantities of these contaminants will be taken up by plants					
Natural die-off	P					
	Natural decay of organisms in an unfavorable environment					

Notes: a P = primary effect, S = secondary effect, I = incidental effect (effect occurring incidental to removal of another contaminant)

b The term metabolism includes both biosynthesis and catabolic reactions

Source: From Tchobanoglou and Culp (1980)

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Table 8.2: Summary of nutrient removal processes in different wetland ecosystems

Wetland type	Nitrogen	Phosphorus
Northern peatlands: good removal	Denitrification Vegetation uptake NH_4^+ adsorption to peat	Adsorption to peat Vegetation uptake
Non-tidal fresh-water marshes: variable removal	Denitrification Macrophytic uptake Periphytic uptake	Chemical precipitation Macrophytic uptake Periphytic uptake Adsorption to substrate
Tidal fresh-water marshes: poor or no removal	Denitrification Vegetation uptake Tidal transfer	Litter uptake Vegetation uptake Tidal transfer
Brackish or salt marshes: variable removal	Denitrification Macrophytic uptake Periphytic uptake Tidal transfer	Macrophytic uptake Periphytic uptake Adsorption to peat Tidal transfer
Southern swamps: good removal	Denitrification Macrophytic uptake Periphytic uptake	Macrophytic uptake Periphytic uptake Adsorption to substrate
Sawgrass marshes: poor removal		Adsorption to substrate Litter uptake

Source: Benforado and Bastian (1985)

Table 8.3: Range of pollutant removal efficiencies reported for wetland treatment systems

	Removal (%)	
	Natural wetland (Sec. Effluent)	Constructed wetland (Pri. Effluent)
BOD ₅	70 - 96	50 - 90
SS	60 - 90	40 - 94
N	40 - 90	30 - 98
P	10 - 50	20 - 90

Source: Revised from Reed and Bastian (1980)

WETLAND ALTERNATIVES FOR MEETING WATER QUALITY OBJECTIVES

Under appropriate conditions, both natural and constructed wetland systems have achieved high removal efficiencies for biochemical oxygen demand (BOD), suspended solids (SS), nutrients (N, P), heavy metals and trace organics (Table 8.3). However, as noted above, the specific factors responsible for the treatment levels achieved are not clearly understood, and criteria applicable throughout the United States are not available for routine design of wastewater treatment systems involving wetlands (Reed and Bastian, 1985).

Rather than a single concept for the involvement of wetlands in wastewater treatment, Reed and Bastian (1985) suggest a continuum of scenarios whereby wastewater and wetlands could be effectively combined as a part of water quality management projects.

Natural Wetlands for Wastewater Disposal

Natural wetlands currently are receiving numerous wastewater discharges - over 400 sewage treatment plants discharge to natural wetlands in the southeast alone. While considerable wastewater treatment may take place in the wetland, these discharges are regulated like any other surface water discharges, and are required to meet water quality standards at the point of discharge.

Wetland Enhancement, Restoration, or Creation

In arid parts of the country it is not uncommon for wastewater effluents to serve as the water supply used to create, maintain, restore, or enhance natural wetlands. In many cases wastewater effluent is the sole or major water source (e.g. the Mt. View Sanitary District project near Martinez, CA, built as an alternative to the deepwater outfall into Suisun Bay, and the Bitter Lake National Wildlife Refuge near Rosewell, NM, which depends on the Rosewell sewage treatment plant effluent as its main supply of freshwater). Some serious environmental problems have occurred in such situations (e.g. the Kesterson National Wildlife Refuge, which received extremely high levels of selenium in the agricultural drainage water from the San Joaquin Valley).

Natural Wetlands for Wastewater Treatment or Reclamation

A number of engineered treatment systems in Michigan, Wisconsin, Florida and elsewhere effectively utilize the capabilities of natural wetlands to provide part of the treatment. These systems attempt to achieve wastewater treatment in a manner that minimizes ecological disturbance. Typically, the only construction activity involved is the installation of the wastewater application system, similar to wetland discharge systems. Such systems require pretreated wastewater, and are usually used to provide for nutrient removal or high level effluent polishing to protect downstream water quality.

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Constructed Systems

The use of constructed wetlands for wastewater treatment shows great promise because of a greater opportunity for process control and less chance for adverse environmental effects. In some cases such systems have been built to simulate natural wetlands, receiving relatively low loadings of pretreated effluents for further polishing while enhancing wildlife habitat and other wetland values (e.g. Arcata, CA; Incline Village, NV; Harriman, NY). In other cases wetland systems have been built and operated to treat high loadings of wastewater in as small an area as possible (Santee and Gustine, CA; Collins, MS; Listowel and Port Perry, Canada; and numerous systems in Germany, Austria, Denmark, England, Australia, and other countries).

PROJECT IMPLEMENTATION PROBLEMS AND LIMITATIONS

Would-be users of wetlands in water quality projects frequently face many technological and practical problems. Unlike the case of conventional wastewater treatment practices and other land treatment technologies, only limited data are available for use in designing wetland systems for wastewater treatment and reuse. This situation is exacerbated by the wide variety of wetland types and possible alternatives for using natural and constructed wetland systems to help achieve water quality objectives, and by the lack of a detailed understanding of many of the physical, chemical, and biological processes of wetland ecosystem dynamics.

Monitoring of wetland systems encounters interesting complications such as where and how to collect representative samples, what to monitor for, and how to interpret results in regard to water quality and environmental impact. Also, water quality may be temporarily or seasonally altered greatly by climatic and other environmental conditions and events, such as short growing seasons, long periods of freezing temperatures, flooding, or other severe weather. Man-made disruptions also occur; construction of access roads, monitoring stations, dikes, weirs, impoundments, and other water control structures can be very difficult and expensive without seriously disrupting large areas in a wetland.

In addition, a number of possibly serious, but hopefully surmountable, problems endanger public acceptance of wetlands water quality projects by neighbors, government officials and special interest groups. Wetlands have historically served as a handy place to dispose of wastes, rather than as integral parts of carefully designed and managed water quality projects. Such practices have led to serious degradation of valuable wetlands, and creates a priori opposition to current efforts.

This situation is complicated by unanswered questions about potential long-term effects. Wetland plant and animal community changes will occur (e.g. species diversity, productivity, successional patterns, or other structural and functional changes) but cannot be adequately predicted. Concerns over the possibility of ground-water contamination, noxious algae blooms or other eutrophication responses, biomagnification of toxins, and wildlife or human disease or contamination problems are often raised when

wetland water quality projects are proposed. Finally, land use issues (e.g. preservation vs. development rights, multiple uses of publicly owned lands) can also create serious economic and legal constraints.

CONCLUSIONS

Despite many problems and limitations, increased development and demonstration of practices which utilize the water quality improvement capabilities of natural and managed wetland systems is merited. The potential for a variety of wetland systems to renovate or reuse treated effluent has been well established. What these systems give up in terms of land requirements, susceptibility to environmental influences and lack of direct operational control, they make up through potential savings in energy, manpower, resources, operations and management costs and benefits (Tchobanoglous, Colt and Crites, 1979; Tchobanoglous and Culp, 1980; Reed, Bastian and Jewell, 1981).

Scientific uncertainties over the long-term benefits and detrimental effects of applying wastewater effluents to wetlands for treatment and/or reuse can only be clarified through more experience with operational systems. The possibilities for linking wastewater management with wetlands preservation or creation, non-point water pollution control, ground-water recharge, streamflow stabilization, and wildlife habitat enhancement alone seem to be worth additional efforts. Coupling wetlands with water quality management projects should provide yet another justification for further research and investigation into the interworkings of both natural and man-made wetland ecosystems. Such efforts will require greater exploration of the concepts and practices needed to manage wetland ecosystems which receive wastewater inputs in a manner compatible with other wetland uses and values. Mitigation measures must be developed to help overcome or avoid unacceptable environmental impacts. The closely coordinated efforts of wetland ecologists, biologists, hydrologists and engineers will be required to address these important issues.

The potential for altering the biotic communities of natural wetlands when including them in water quality management projects must be recognized. The variability in performance described for different wetland systems needs to be further explored. Appropriate management practices and adequate monitoring, as well as proper regulation and control of projects, must be developed to help avoid problems from developing. The US Environmental Protection Agency is working with other agencies to establish wetlands management practices and water quality criteria that could be applied in this area. Efforts are underway to fund additional wetland water quality research initiatives and to develop technical guidance for use in developing wetland wastewater treatment projects.

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Chapter Nine

ANALYSIS OF FLOOD PEAK MODERATION BY DEPRESSATIONAL WETLAND SITES

John M. Kittelson

INTRODUCTION

This paper presents the results of a hydrologic analysis of seven wetland sites in Minnesota and Wisconsin. All seven sites are in topographic depressions and have relatively small upstream watersheds. These 'depressional wetlands' are widespread in the prairie pothole region of the US and Canada. They are of hydrologic interest because flooding problems in the region can be severe and because evidence indicates that drainage of depressional wetlands exacerbates these problems (Moore and Larson, 1979).

Methods used in this analysis are based on standard hydrologic modeling techniques and were developed as part of a wetland evaluation methodology designed to assess a variety of wetland functions in the north-central region of the United States. These methods are unique in that they have been structured to provide a relatively simple and rapid means of computing an inflow and outflow hydrograph for an evaluation site. The result is a firm quantitative basis for examining a wide variety of wetland hydrologic characteristics, including the characteristics of flood flows through a wetland site.

In addition to the hydrologic analysis of the seven wetland sites, this paper describes the hydrologic model used in the analysis, discusses its accuracy and the meaning of the results, and describes the mechanisms by which depressional wetlands modify flood flows.

METHODS

Selection of Wetland Sites

The seven wetland sites in Minnesota and Wisconsin (Figure 9.1) are in topographic depressions with small upstream watersheds (less than 25 square miles) and have a variety of outlet types and wetland-to-watershed-area ratios (Table 9.1). Although most of these sites would not be classified as prairie potholes, they are depressional sites with hydrologic characteristics similar to those of prairie pothole wetlands.

Figure 9.1: Location of evaluation sites



Hydrologic Model

The hydrologic model used in the analysis is based on standard hydrologic methods used by the Corps of Engineers (COE) for design of interior drainage ponding facilities and by the Soil Conservation Service (SCS) for design of small water-control structures. The standard methods were streamlined and computerized so that only those computations necessary for hydrologic characterization of depressional wetland sites are in the model.

The model has three components corresponding to the principal hydraulic and hydrologic processes governing flood flows: (1) rainfall (computation of a rainfall distribution), (2) runoff (amount and temporal distribution of runoff from the watershed), and (3) site hydraulics (modification of flow by the depressional site). The following descriptions summarize the required input data and methods used to model each component (refer to Figure 9.2).

Rainfall Distribution

The amount and temporal distribution of rainfall over the wetland's upstream watershed must be known to determine the expected amount and temporal distribution of runoff entering the wetland. The temporal distribution of rainfall assumed for these analyses is a standard type used by the COE (Figure 9.3). This type of distribution produces the maximum amount of runoff for a given

Figure 9.2: Major components and input variables for the hydrologic model

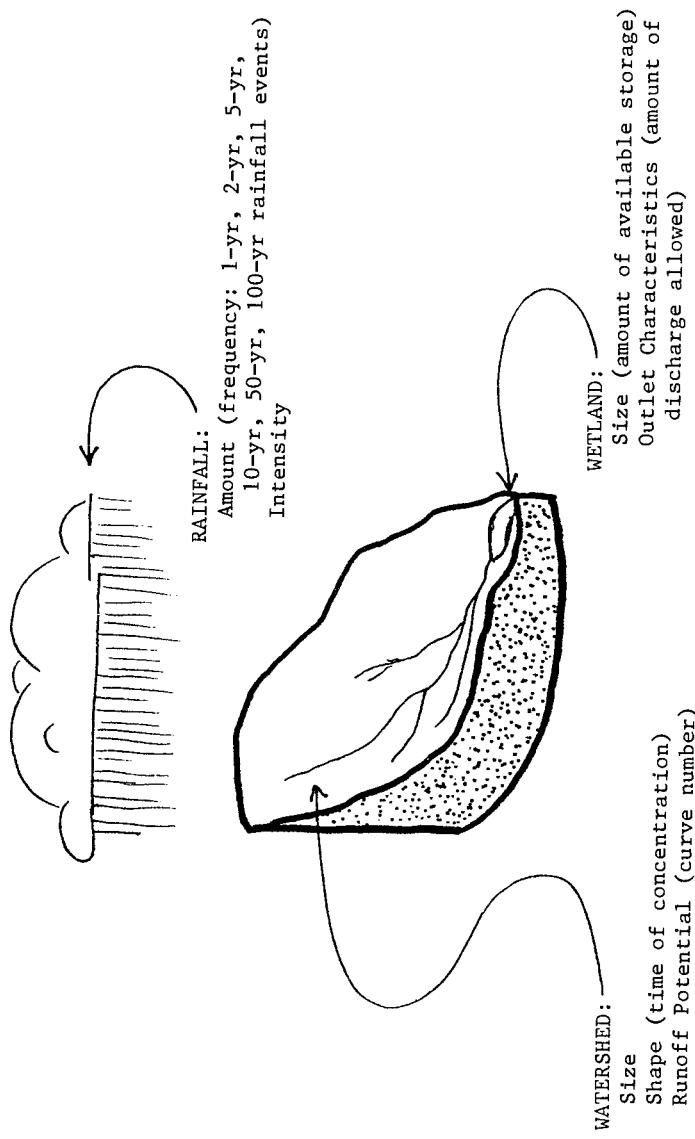


Table 9.1: Evaluation site characteristics

Wetland site	Watershed size (acres)	RCN	Wetland size (acres)	Outlet description
1. Polk County	1791	75.2	61	Road embankment with culvert
2. Fish Lake	540	71.4	5	Low sidewalk with culvert
3. Red Cedar Lake	1390	75.3	340	Broad channel with wetland vegetation
4. Lake Elmo	1418	71.2	50	Road embankment with culvert
5. North Albertville	237	76.3	8	Road embankment with culvert
6. South Albertville	74	76.7	5	Road embankment with culvert
7. Mount Normandale Lake	5333	72.0	118	Earth dam with 20 ft weir

Note: a, runoff curve number

rainfall event, thereby simulating conditions during the more severe flooding situations.

Rainfall amounts vary geographically and with the probability of the event (extremely large rainfalls are rare, whereas moderate storms are more common). Rainfall amounts are required as inputs for each analysis and are readily available from a series of National Weather Service maps (NWS, 1961, 1964, 1977).

Watershed Runoff

The amount and timing of runoff from the watershed (inflow hydrograph) resulting from a given rainfall event is computed using relationships between the size and shape of the watershed and its absorptivity (a function of land use). The SCS method (SCS, 1972) is used for computation of the inflow hydrography, and requires the following inputs.

- (1) Rainfall distribution computed in the previous step.
- (2) Watershed size (square miles).
- (3) Time of concentration (an indicator of watershed size).

$$\text{time of concentration} = 0.0078 (L^{1.5} H^{-0.5})^{0.77} \text{ (Kirkpich, 1940)}$$

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Where H = drop in elevation (measured in feet) from the hydrologically most remote point in the watershed to the site outlet;

L = distance (feet) along stream channels that water must travel between the hydrologically most remote point and the site outlet.

(4) Runoff curve number (RCN):

$$RCN = 8OU + 80W + 75A + 60F$$

Where: U = proportion of the watershed that is urban land;

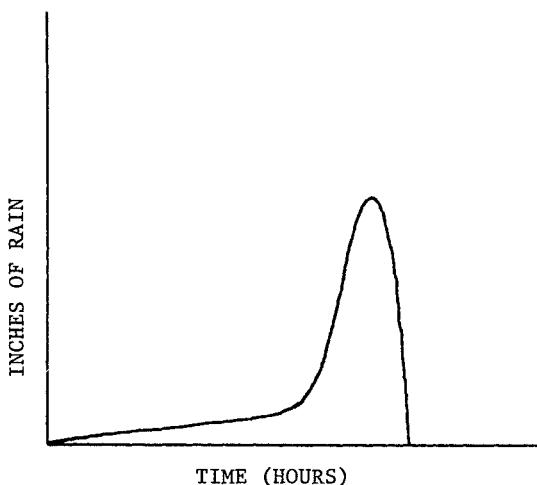
W = proportion of the watershed that is wetland or lake;

A = proportion of the watershed that is agricultural land, including pasture;

F = proportion of the watershed that is forested or natural vegetation, including grassland

This is a modification of the formula suggested by Ammann, Franzen and Johnson (1984).

Figure 9.3: Form of rainfall distribution used in the analysis



Site Hydraulics

The primary influence on flows passing through the wetland are the topographic characteristics of the depression containing the wetland. Characteristics necessary for describing site effect on flows include the capacity of the site's outlet and the volume available for storage of flood water.

An outflow hydrograph for the site is computed by routing the inflow hydrograph through the wetland using the Modified Puhl's procedure (Chow, 1964, pp. 25-38). The following inputs are required:

- (1) Inflow hydrograph computed in the previous step.
- (2) Volume/elevation relationship - Total volume of storage in the depression at various elevation increments can be computed with estimates of surface area of the site at two elevations:

$$\text{total volume} = (h/3)(a_i + a_b + (a_i a_b)^{0.5})$$

Where : h = the elevation difference between elevation 'i' and the lowest elevation;

a_b = surface area estimate at the lowest elevation;

a_i = surface area at elevation 'i'.

Surface area is assumed to increase linearly with elevation; hence a_i is computed as follows:

$$a_i = a_b + (h/H)(a_t + a_b)$$

Where : a_t = acreage estimate at highest elevation;

H = elevation difference between the two acreage estimates.

- (3) Discharge/elevation relationship - Flow through the site outlet is computed at various elevation increments by determining the elevation of the lowest point in the outlet, placing the outlet in one of the following categories, and making the indicated measurements.
 - (a) Channel-type outlets - construct a cross section of the channel at the outlet and determine discharge using Manning's equation (Chow, 1964, pp. 15-32).
 - (b) Weir-type outlets - measure weir length at the minimum of two elevations and compute discharge using the weir equation (Brater and King, 1976).
 - (c) Culvert-type outlets - determine culvert type (e.g. cement-round, cement-arched, corrugated metal), make necessary measurements (e.g. culvert diameter), and compute discharge using culvert nomographs (FHWA, 1978 - note: inlet control is assumed).

Computer Program

An interactive computer program enables rapid computation of inflow and outflow hydrographs for the depression containing the wetland. The program runs on any MS-DOS computer with a minimum of 256K of RAM. Much of the basic source code was extracted from the HEC-1 hydrology package (COE, 1981).

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Input variables for the program are derived from the variables just described. Outputs include inflow and outflow hydrographs for the depression containing the wetland for seven rainfall events (Figure 9.4). An overall rating of the magnitude of change in peak flood flow across the site is computed by analyzing the predicted reduction in peak flow for all rainfall events (Tables 9.2 and 9.3).

RESULTS

The results of the analyses are described below and are summarized in Tables 9.2 and 9.3.

1. Polk Country Wetland. Outflow from the wetland is controlled by a road embankment and a culvert. The model predicts the road embankment will contain everything below the 25-year flood (probability of occurrence = 0.04), above which the road is overtopped and outflow increases dramatically (Figure 9.4).
2. Fish Lake Wetland. Outflow from this small wetland is controlled by a low sidewalk and culvert. The model indicated the sidewalk will be overtopped during floods greater than the 1-year flood. Outflow is basically unrestricted: hence, the average annual reduction in peak flow is quite low.
3. Red Cedar Lake. Two outlets control outflow from this site: a 300-foot wide channel and a 5-foot wide channel. Since the wetland is so large in comparison to the watershed, peak moderation is high in spite of the large outlet capacity.
4. Lake Elmo Wetland. Outflow is controlled by a high roadway embankment and a culvert. Flows never come close to overtopping the road, and flood peak moderation is therefore very high.
5. North Albertville. Outflow is controlled by a roadway embankment and culvert. Inflow to the site passes through the South Albertville site; hence, inflow amount may be much less than actually computed by the model.
6. South Albertville. Outflow is controlled by a high roadway embankment and culvert. Even though the roadway embankment is not overtopped, the culvert is large enough to allow substantial outflow. Hence, peak flow moderation is not as high as might otherwise be expected.
7. Mount Normandale Lake. Outflow is controlled by a dam containing a broad-crested weir (20 feet long). Discharges over the weir are substantial during all rainfall events; and during large events (50-year and 100-year events) the dam is overtopped. Because the watershed in this analysis could be termed 'hydrologically diverse' (see Discussion section), inflow volumes may be overestimated by the model.

Figure 9.4: Inflow and outflow hydrographs for the Polk County site

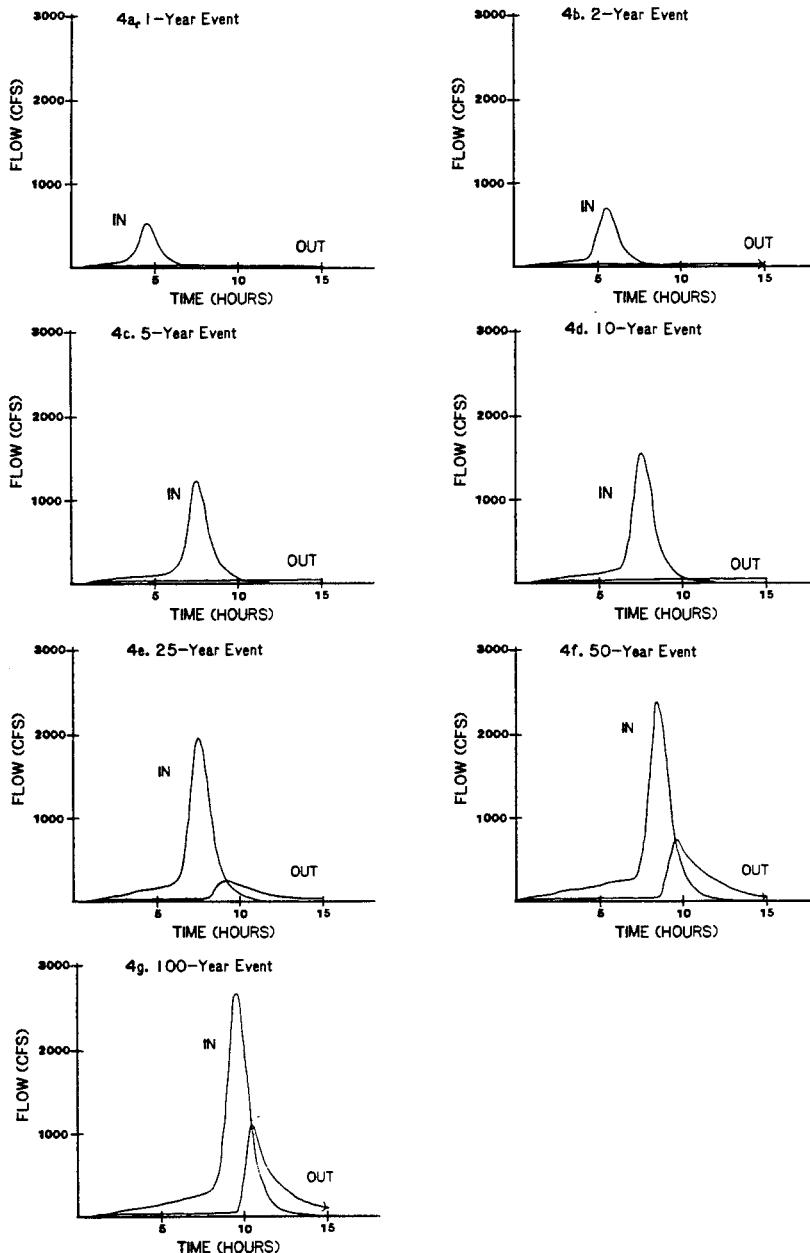


Table 9.2: Peak inflow and outflow (cubic feet per second) for all evaluation sites and rainfall events ^a

Wetland site		1-yr.	2-yr.	5-yr.	10-yr.	25-yr.	50-yr.	100-yr.
1. Polk	In Pk	520	700	1,200	1,520	1,940	2,350	2,640
	Out Pk	25.1	28.0	34.3	37.4	229	680	1,030
2. Fish	In Pk	188	261	470	592	759	924	1,070
	Out Pk	142	219	468	582	737	900	1,050
3. R. Cedar	In Pk	549	725	1,580	1,930	2,580	2,970	3,330
	Out Pk	2.65	3.49	10.3	12.2	18.8	21.8	23.6
4. L. Elmo	In Pk	421	575	1,060	1,330	1,690	2,070	2,370
	Out Pk	3.18	4.17	6.93	8.05	9.42	10.0	10.3
5. N. Alb.	In Pk	113	144	288	368	468	559	638
	Out Pk	0.00	0.00	3.40	7.12	11.6	17.1	18.6
6. S. Alb.	In Pk	65.0	82.0	173	228	291	330	376
	Out Pk	13.6	15.7	37.7	51.6	65.6	74.4	80.6
7. M. Norm	In Pk	1,000	1,380	2,350	3,030	3,910	4,630	5,290
	Out Pk	187	287	948	1,640	2,460	3,090	3,640

Note: a, Rainfall events are defined according to their probability of exceedence. For example, the 25-yr. event refers to the amount of rainfall which would be exceeded only once in 25 years.

Table 9.3: Average annual peak inflow and outflow (cubic feet per second)^a

Wetland site	Average annual peak inflow	Average annual peak outflow	Average annual difference	Reduction (%)
1. Polk	897	51.8	845	94
2. Fish	342	311	31.0	9.1
3. R. Cedar	1,062	6.29	1,056	99
4. L. Elmo	766	5.07	759	99
5. N. Alb.	203	2.06	201	99
6. S. Alb.	120	25.3	95.0	79
7. M. Norm	1,770	645	1,120	64

Note: a, Average annual peak is computed by plotting peak flow against the probability of that flow and computing the area under the resulting curve

DISCUSSION

Model Assumptions

The model used in the analysis is based on the following assumptions.

- (1) Uniform spatial distribution of rainfall - rainfall is assumed to fall evenly over the entire site and its upstream watershed.
- (2) Hydrologically uniform watershed - the watershed upstream of the wetland site is assumed to be hydrologically uniform. Diverse watersheds are those that can be divided into two or more subwatersheds, that have significant upstream storage (lakes, ponds, etc.), or that have a marked non-uniform distribution of land use types.
- (3) Site functions like a reservoir - water flowing into the depression is assumed to form at least a small pool and either be stored or flow out of an outlet (not necessarily a man-made outlet).

Assumptions (1) and (3) are almost always met; however, some depressional sites will not meet assumption (2). Assumption (2) restricts the analyses to watersheds that have runoff hydrographs with only one peak. Presence of two or more subwatersheds, uneven distribution of land use, or the presence of upstream storage could all result in hydrographs with more than one peak. Assumption (2) is strict in the sense that, if it is not met, the results may be meaningless.

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Reasonableness of Results

Water surface elevations within the depression are predicted by the model using inflow and outflow rates. The reasonableness of the model can be judged by comparing the predicted water surface elevations to land use and vegetation types surrounding the site (e.g. if the model predicts an adjacent housing development would be flooded each year, the results are probably unreasonable).

When analyzed according to predicted water surface elevations, the model results are reasonable for all sites evaluated. Initial application of the model at Mount Normandale Lake indicated water levels would be high enough to flood an adjacent highway on a regular basis. A closer look at the site revealed that much of what had been considered watershed was actually non-contributing. Reanalysis using a smaller watershed size produced more reasonable results.

Flood Peak Moderation

There is a distinction between the wetland and the depression containing the wetland in the moderation of peak flows. Although flood peak moderation is commonly referred to as a wetland function (Adamus and Stockwell, 1983; OMNR, 1983; Ammann et al, 1984; and others), it is actually controlled by topographic variables. Peak moderation is a physical process that happens to occur at a wetland site rather than a function of the wetland itself.

This interpretation does not imply that wetland characteristics do not influence flood flows. On the contrary, wetland vegetation type, evapotranspiration rates, and ground-water losses or discharges occurring in the wetland will affect the peak moderation characteristics. In spite of this, it must be remembered that topographic effects are basic to the peak moderation process in the sense that they determine the degree to which other characteristics influence flows.

The model used for this analysis includes the effect of upland portions of the outlet and storage available over upland areas that are adjacent to the wetland. Conclusions drawn from the analyses should therefore be considered a description of a physical process (moderation of peak flows) occurring in a topographic depression that contains a wetland.

Results of the analyses indicate that the change in peak flows attributable to a site varies according to the interaction between outlet capacity, storage available within the site, and the amount of water coming into the wetland. The Lake Elmo and North Albertville sites show that a highly constricted outlet which is never overtopped has a dramatic effect on flood peaks of all sizes (99 per cent average reduction in peak flows). Wetland sites that have a constricted outlet at lower elevations but an unrestricted outflow at higher elevations provide good flood storage up to the point of unrestricted outflow. Two evaluation sites demonstrate this characteristic: (1) the Polk County wetland has basically unrestricted flow on large flood events, but contains all small events (94 per cent average annual reduction in peak flow); and (2) the Fish Lake wetland has constricted outflow only on the lowest flood events (9 per cent reduction in peak flows).

The evaluation at Red Cedar Lake shows that a large wetland-to-watershed-area ratio can also result in significant moderation of peak flows even with a high capacity outlet. At this site, inflow water is spread in a thin layer over the entire wetland surface and does not increase outflow even though the outlet is basically unrestricted.

The effects of a moderate outlet are demonstrated at Mount Normandale Lake (64 per cent reduction in peak flows). The outlet for this site is a dam with a 20 foot weir that was constructed for the specific purpose of flood control. Note that this site did not have one of the higher ratings of average reduction in peak flows, which demonstrates that ratings produced in this analysis do not provide an indication of downstream peak reduction values. It is very probable that the predicted 64 per cent reduction in peaks (as measured at the site outlet) is adequate for prevention of downstream flood damages and that higher reductions would have no additional effect on those damages.

Downstream and Cumulative Effects

This analysis focuses on the description of peak moderation at the outlet of the depression containing the wetland, and provides no indication of the significance of the predicted peak reduction in terms of reducing downstream flood damages. It also gives no indication of the cumulative effect on peak flows resulting from the presence of many depressional wetlands in a watershed. Modeling either of these effects is very data intensive and is clearly beyond the scope of a rapid assessment model such as the one presented.

In lieu of detailed characterization of downstream or cumulative effects, it may be possible to identify ranges or threshold values below which additional losses of depressional storage sites would result in significant increases in downstream flows. Identification of threshold values may be possible using regression analysis on USGS watershed data (Novitzki, 1978); however, this work is very preliminary and is not yet useful for this purpose.

SUMMARY

The hydrologic characteristics of seven wetland sites in Minnesota and Wisconsin were analyzed using standard hydrologic modeling procedures. The methods used were developed as part of a wetland evaluation methodology, and provide a rapid means of computing an inflow and outflow hydrograph for depressional wetland sites.

The analyses indicate that the change in peak flows attributable to a wetland site vary according to the interaction between outlet capacity, storage available within the site, and the amount of water coming into the wetland. The model indicates that wetland sites with highly constricted outlets that contain all flows are very effective at reducing peak flow. Sites with constricted outlets at lower elevations and unrestricted outflow at higher elevations will reduce peak flow until the point of unrestricted outflow is reached. Outlet effects are also related to the effect of storage volumes, as demonstrated in the analyses of Red Cedar Lake where

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large amounts of storage result in significant reductions in peak flows in spite of unrestricted outflow.

The model used in the analysis produced reasonable results as judged through comparison of predicted water surface elevations with land use and vegetation types surrounding the site. The model focuses on the effects of topographic variables because they are of primary importance to the moderation of peak flows. All estimates produced in the analysis are effects predicted at the site outlet and do not provide an indication of the effect of peak reduction on downstream flood damages. Quantitative treatment of downstream flood damage is not feasible in a rapid assessment framework, although it may be possible to develop regression equations that would be of some use.

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Chapter Ten

PHYSICAL AND BIOLOGICAL CONTROL OF MANGROVE PORE WATER CHEMISTRY

Paul R. Carlson, Jr and Laura A. Yarbro

INTRODUCTION

Mangrove swamps comprise the largest fraction of tropical and subtropical intertidal wetlands, occupying over 20 million hectares worldwide (Chapman, 1976; McVey and May, 1987). Their importance as the basis of detrital food webs and as protected habitat for juvenile fish and shellfish has been well documented (Odum and Heald, 1972; Rodelli, Gearing, Gearing, Marshall and Sasekumar, 1984).

Despite the importance of mangrove communities, many major aspects of their functional ecology are poorly understood. The physiological ecology of the mangrove species and their abilities to tolerate salt, flooding, and anaerobic sediments are important areas of investigation because of the pressure on coastal wetlands for reclamation and the apparent sensitivity of mangroves to anthropogenic stresses. Sediment chemistry is important to agricultural and aquacultural interests because acid sulfate soils have developed throughout the world when mangrove areas have been reclaimed. At the other end of the spectrum, protection of mangrove habitats as a fisheries resource and restoration of impacted wetlands also require detailed knowledge of the physiological ecology and stress tolerance of mangrove species.

Recent work in temperate salt marshes indicates that wetland plants have a number of marked effects on marsh sediment chemistry (Howarth and Hobbie, 1982). Rather than passive elements of chemical systems, plants may be active geochemical agents in a variety of ways. McGovern, Laber and Gram (1979) and Carlson (1980) demonstrated that sulfate is excluded at the root surface by transpiring *Spartina alterniflora*, thereby increasing the sulfate:chlorine ratio of marsh pore water. Transpiration by plants causes mass flux of water into marsh sediments (Giurgevich and Dunn, 1979; Dacey and Howes, 1984; see Chapter 41). Leakage of dissolved organic matter from *Spartina* roots may also stimulate sediment heterotrophic bacteria and accelerate sulfate reduction rates (Howarth and Hobbie, 1982). The diffusion of oxygen out of wetland plant roots into the surrounding sediments may inhibit obligate anaerobic sulfate-reducing bacteria from producing sulfide or it may oxidize sulfide after it is produced. The term bioturbation has been widely used to describe the effects of burrowing

organisms on sediment chemistry, but we will expand its definition to include the effects of plants, as well.

We investigated the relationships between mangroves and sediment chemistry because we anticipated that the high plant biomass to sediment volume ratio in mangrove forests would magnify the bioturbative effects observed in temperate salt marshes. This chapter is divided into two sections: the first reports the results of seasonal studies of pore water chemistry, while the second part describes experimental studies to separate biological effects of the mangroves on sediment chemistry from physical factors such as tidal inundation frequency.

SEASONAL STUDIES OF MANGROVE PORE WATER CHEMISTRY

Seasonal studies of pore water chemistry were conducted during calendar year 1981 on an overwash island mangrove community (*sensu* Lugo and Snedaker, 1974) in the Indian River lagoon near Fort Pierce, Florida. The island, termed the ISL site, has a monotypic fringing zone of Rhizophora mangle 10-30 m wide, a central zone with a canopy of Avicennia germinans and a subcanopy of Rhizophora mangle 70-100 m wide, and a total area of approximately 4.8 ha.

The Indian River is a bar-built lagoon along the east coast of Florida (Figure 10.1). The lagoon is approximately 200 km long, stretching from Titusville, FL (lat. $28^{\circ} 37'$, long. $80^{\circ} 48' W$) to Stuart, FL (lat. $27^{\circ} 10' N$, long. $80^{\circ} 11' W$). Prior to hydrologic alterations, the lagoon was euhaline to slightly hypersaline. Increased freshwater drainage from agricultural areas and limited exchange with the Atlantic Ocean now cause large salinity excursions from ca. 40 ppt in the dry season (October-May) to less than 10 ppt after heavy rainfall periods during the wet season (June-September).

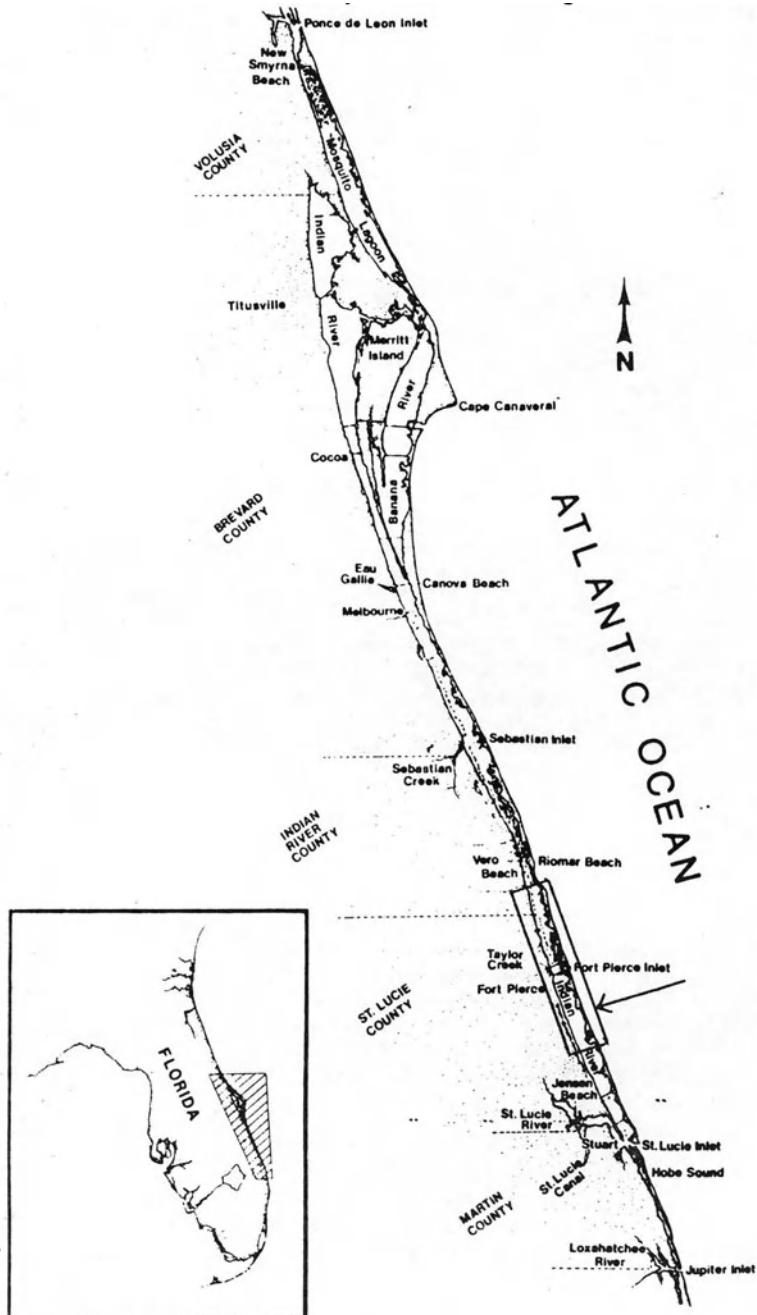
Tidal range within the Indian River declines rapidly with increasing distance from inlets (Smith, 1983). Mean tidal range at Fort Pierce inlet is 78 cm (National Ocean Survey, 1985), while the mean tidal range within the Indian River at Vero Beach, 12 km north of the Fort Pierce Inlet, is 21 cm (Provost, 1973a). Superimposed on this low tidal range is a seasonal cycle of variation in local mean sea level (LMSL) which causes marked seasonal differences in the frequency and duration of tidal inundation of mangroves within the lagoon. Seasonal variations in LMSL (22.5 cm) can exceed the annual mean tidal range for much of the Indian River. Highest LMSL values occur in September and October, and lowest levels occur in April and July.

Methods

Tidal inundation frequency at the ISL site was determined by correlation of tide heights at the study site with continuous water-level recordings from a tide gauge 3.4 km northwest of the study site. Hypsometric elevation surveys of the ISL site were made during protracted inundation periods during the fall.

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Figure 10.1: The Indian River Lagoon and adjacent waters. Study area denoted by arrow, lower right



We collected pore water at the ISL site from arrays of samplers in the central, Avicennia-dominated, portion of the island (termed the AVI zone) and from the monotypic fringe of Rhizophora (the RHI zone). Samples were collected at intervals of one to four weeks in porous Teflon samplers under an argon atmosphere (Montgomery, Zimmerman and Price, 1979) at 10, 20, 30, 40 and 50 cm depth. Pore water salinity, sulfate, chloride, iron, and sulfide concentrations were determined using the methods of Carlson, Yarbro, Zimmerman and Montgomery (1983). Surface water salinity and temperature were also measured on each sampling date.

Redox profiles were determined in each zone by using an epoxy 'stick' electrode (30 cm long) with a short (ca. 1 cm) piece of platinum wire (1.0 mm diameter) embedded in the tip. The electrode was inserted into the sediments adjacent to a double-junction reference electrode (orion Model 90-02) immersed in pore water or surface water. After insertion to a specified depth, the platinum electrode was allowed to stabilize for 30 s before readings were taken using an Orion Model 231 pH/mv meter. Values are reported as ORP (oxidation-reduction potentials) without pH, temperature or ionic strength corrections. ORP values are similar, but not identical, to Eh values.

All statistical tests, including Pearson's correlation coefficients, were performed using SAS (SAS Institute, 1985). Despite heterogeneity of variances, Duncan's multiple range tests were performed because one-way ANOVAs produced very high F-ratios.

Results

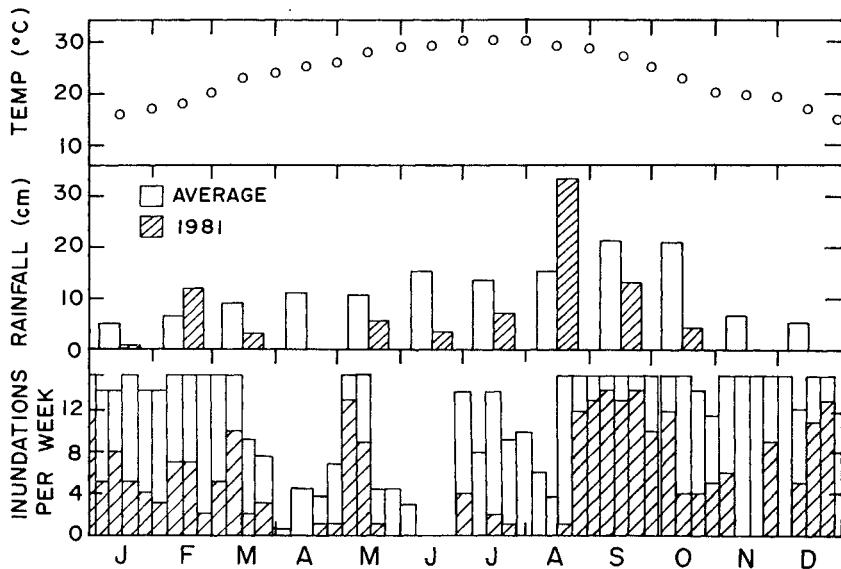
An elevation survey of the ISL site showed that the lower distribution limit of Rhizophora mangle was approximately equal to LMSL for the island during the calendar year 1981. The upper boundary of the monotypic Rhizophora fringe (hence the lower limit of Avicennia pneumatophore distribution) was +15 cm relative to LMSL. Elevations across the Avicennia-dominated central zone of the island varied less than 5 cm. Mean tidal range for the ISL site during calendar year 1981 was 28.6 cm, placing the AVI zone 2 cm above LMHW.

The small difference in elevation (15 cm) between the RHI and AVI zones resulted in pronounced differences in tidal inundation frequency, most evident in spring and summer (Figure 10.2), when only spring tides or wind tides were high enough to flood the AVI zone. During the fall, however, inundation frequency and duration were high for both zones, and the island was flooded continuously for periods up to one week during new and full moon phases. Over the entire calendar year the RHI zone was flooded 534 times (73 per cent of all high tides) whereas the AVI zone was flooded only 255 times (or 35 per cent of all high tides).

A cooling trend began with the passage of tropical storm Dennis in mid-August. Dennis also doubled the amount of rainfall in August over the 30-year mean value and offset drought conditions which had occurred during the spring and early summer (Figure 10.2). Separation of salinity and tidal inundation effects was made difficult by dramatic coincident changes in both par-

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Figure 10.2: Physical data for seasonal studies, calendar year 1981. (a) Monthly mean surface water temperature; (b) Rainfall: open bars, 30 year average; cross-hatched bars, 1981; (c) Tidal inundation frequency, open bars represent Rhizophora zone; cross-hatched bars superimposed on open bars represent Avicennia zone



Source: (b) National Weather Service, Vero Beach airport recording station

ameters during late summer 1981 (Figure 10.2, Table 10.1). Monthly mean water temperature rose from 15°C in January to nearly 30°C in July (Figure 10.2).

Pore water chloride (Figure 10.3) and sulfate (Figure 10.4) concentrations in both zones were higher than concentrations in the surface water of the Indian River lagoon throughout the year. Enrichment was greatest at mid-depths in both zones during July and August, but enrichment affected a larger portion of the sediment column and lasted longer in the AVI zone than in the RHI zone. Peak chloride concentrations greater than 32 ppt were measured at mid-depths in the AVI zone during July and August. These values are 70 per cent greater than the chlorinity (19.16 ppt) of standard 35.6 ppt seawater. Peak sulfate concentrations (greater than 60 mM) were more than double standard seawater values.

In oxygenated surface waters, the sulfate:chlorinity ratio of seawater is virtually constant throughout the world's oceans and is considered a conservative property of seawater, not influenced by

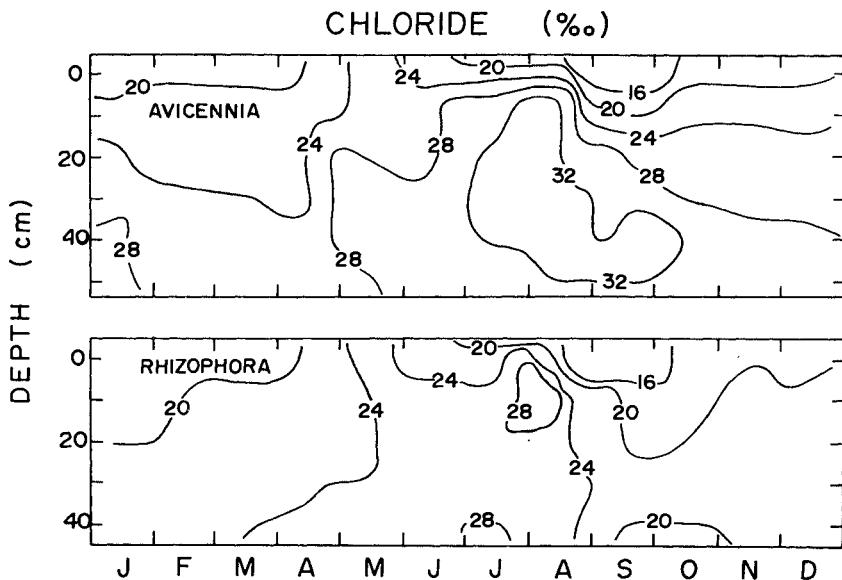
Table 10.1: Correlation of tidal inundation frequency, salinity, temperature with physicochemical parameters in mangrove sediments. N for most parameters is 15. $\text{L}_{\text{Fe}} = \log_{10}$ dissolved iron (μM)

Zone	Depth(cm)	Physical variable			Pore water parameter			
		IF	ORP	pH	S=	L_{Fe} ^a	Cl^-	SO_4^{2-}
AVI	10	0.93 ^b	-0.86 ^a	0.29	0.83 ^b	-0.71 ^a	-0.59 ^a	
		0.56	0.07	-0.50	-0.52	0.89 ^b	0.97 ^b	
		0.38	-0.57	-0.11	-0.19	0.39	0.60 ^a	
AVI	30	-0.57	-0.98 ^b	-0.10	0.58	0.10	0.04 ^b	
		0.33	0.01	-0.36	-0.35	0.97 ^b	0.94 ^b	
		0.37	-0.25	0.12	-0.50 ^a	0.65 ^b	0.88 ^b	
RHI	10	-0.30	-0.35	0.31	0.88 ^b	-0.78 ^b	-0.72 ^a	
		0.36	0.59 ^a	-0.44	-0.24	0.88 ^b	0.66 ^a	
		0.25	-0.16	-0.13	0.26	0.31	0.51 ^a	
RHI	30	0.13	0.22	0.41	0.58	-0.47	-0.46 ^a	
		-0.36	0.38	-0.36	-0.07	0.85 ^b	0.93 ^a	
		-0.47	0.01	-0.14	-0.20	0.44	0.74 ^b	

Notes: a, a=0.05; b, a=0.01

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Figure 10.3: Pore water chloride expressed as gCl⁻ per liter pore water. Data are time-depth isopleths of concentration. See text for details of sampling depths and frequency. Top panel represents Avicennia zone, lower panel Rhizophora zone

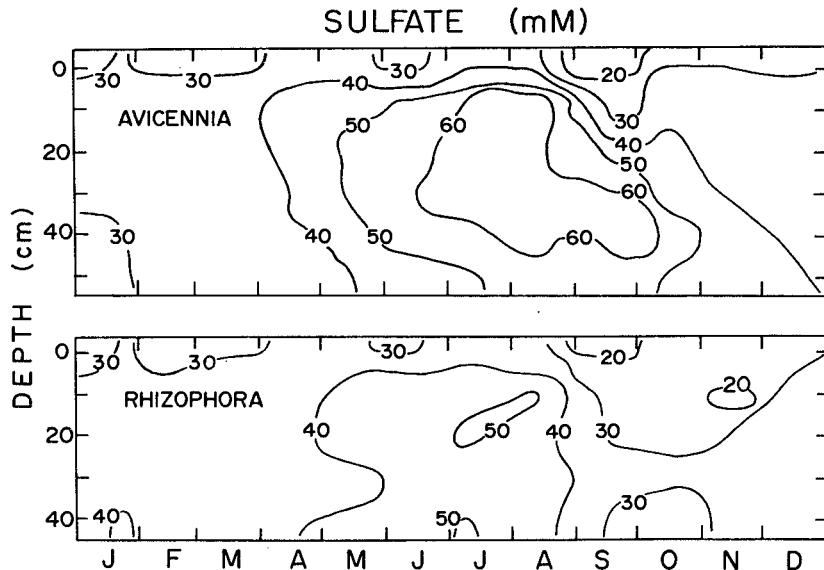


dilution or evaporation. Sulfate:chlorinity ratios in pore water, when normalized to the ratio of standard seawater (Figure 10.5), showed that sulfate was concentrated in the pore water of both zones to a greater degree than chloride, indicating that some mechanism other than evaporation was responsible for the enrichment. The extent of the enrichment in time and space was greater in the AVI zone than in the RHI zone.

Selective exclusion of sulfate at the root surface by mangroves during uptake of pore water for transpiration was established as the mechanism responsible for the large increases in the pore water sulfate:chlorinity ratio when we analyzed the salts excreted on the surface of Avicennia leaves and found they were extremely depleted in sulfate relative to both lagoon water and pore water. Other physical, chemical, and biological processes could not account for the large increases in pore water sulfate which we observed. Mangrove transpiration is therefore a major bioturbative influence on sediment chemistry.

Relationships of inundation frequency, salinity, and temperature with pore water parameters are complex and vary with sediment depth and zone (Table 10.1). Inundation frequency was significantly and negatively correlated with chloride at 10 cm in both zones and also with sulfate at 10 cm in the RHI zone, but

Figure 10.4: Pore water sulfate concentrations expressed as millimoles sulfate per liter. Panels and sampling data as described for Figure 10.3



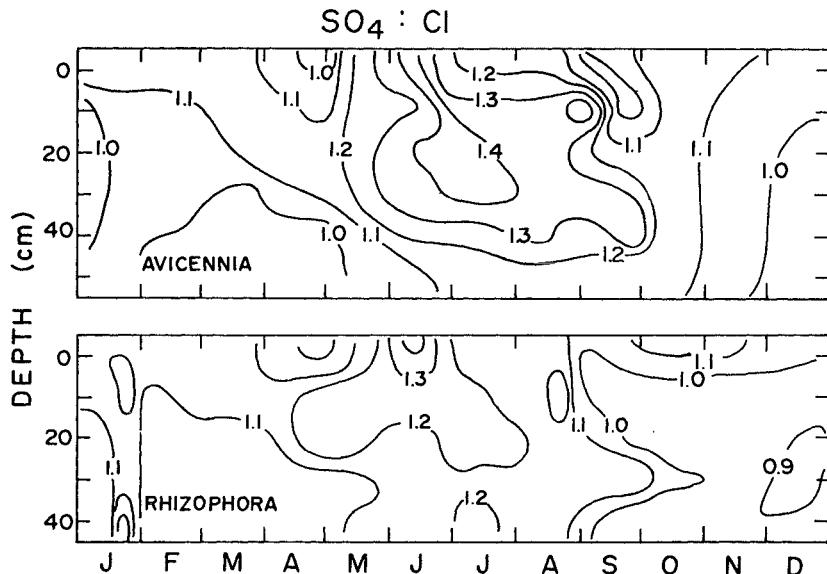
showed little relationship with pore water parameters at 30 cm depth in either zone. Correlations of salinity with chloride and sulfate at both 10 cm and 30 cm in both zones were positive and significant. Temperature was significantly correlated with sulfate at both depths in both zones. Any direct effects of temperature may be obscured by the coincidence of low inundation frequency with high temperature (Figure 10.1) and high evapotranspiration rates. These data suggest that the bioturbative effects of mangrove transpiration dominate subsurface pore water chemistry while tidal inundation frequency and salinity probably control the chemistry of surface sediments to a depth of 10 cm.

Highest sediment ORP values (uncorrected for pH or ionic strength variations) occurred in the upper 20 cm of both zones during the spring and summer 'dry-down' period, when tidal inundation frequency was low (Figure 10.6). Lowest ORP values occurred during the fall when inundation frequency was greatest. ORP values were always higher at any given depth in the AVI zone than in the RHI zone and generally declined as depth increased in both zones.

Pore water sulfide concentrations were much lower in the AVI zone than in the RHI zone (Figure 10.7) and generally varied positively with the seasonal pattern of inundation frequency (cf. Figure 10.2). Sulfide concentrations in the upper 40 cm of AVI sediments were quite low (<100 μ M) throughout the year and

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Figure 10.5: Pore water sulfate:chlorinity ratios. Normalized to standard seawater, molar $\text{SO}_4^{2-}:\text{Cl}^-$ ratio of 5.14×10^{-2} . Values > 1.0 indicate enrichment of SO_4^{2-} , while values < 1.0 indicate sulfate depletion



generally fell below 10 μM . Highest sulfide concentrations (approx. 100 μM in the AVI zone and 1500 μM in the RHI zone) occurred in the fall flood period. Lowest values occurred in spring and summer during the dry-down period.

Pore water iron concentrations also followed the seasonal pattern of tidal inundation frequency with peak values occurring in late August and early September when frequent inundation had resumed after the summer dry-down period (Figure 10.8). Concentrations in AVI sediments ranged from $< 1 \mu\text{M}$ to over 1 mM. The latter value is extremely high for marine sediments, and suggests that low sulfide concentrations are due to low sulfate reduction rates rather than precipitation of iron sulfides. High dissolved iron solution concentrations would not be observed if sulfate reduction rates were high because iron would be scavenged by the high sulfide concentrations. Positive correlations of iron concentrations with tidal inundation frequency at 10 cm in both AVI and RHI sediments were highly significant, while correlations for deeper sediments were not (Table 10.1).

Conclusions

Mangrove transpiration clearly had a drastic effect on pore water chloride and sulfate concentrations, and mangroves may exert

Figure 10.6: Sediment oxidation-reduction potentials. Panels and sampling data as described for Figure 10.3

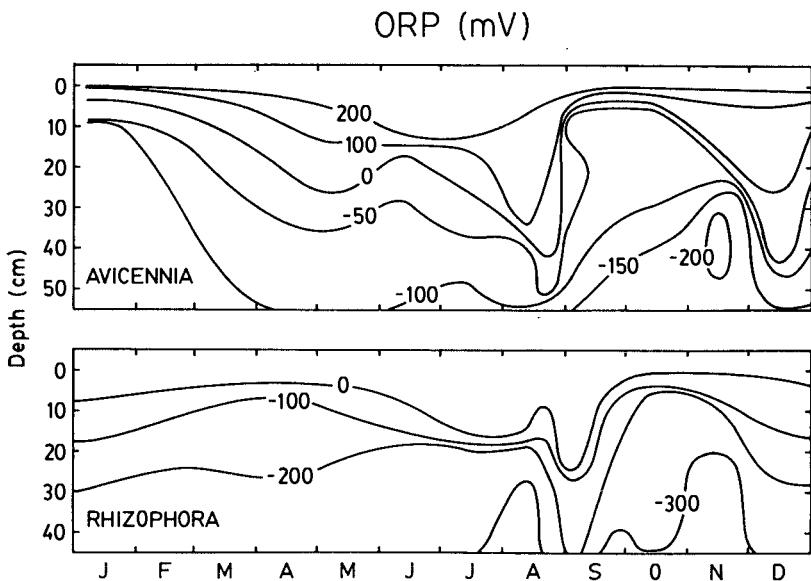
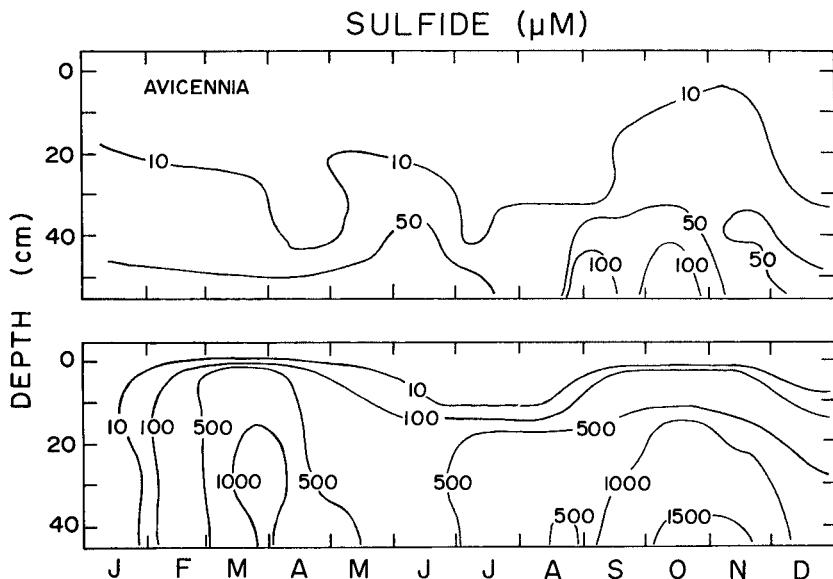
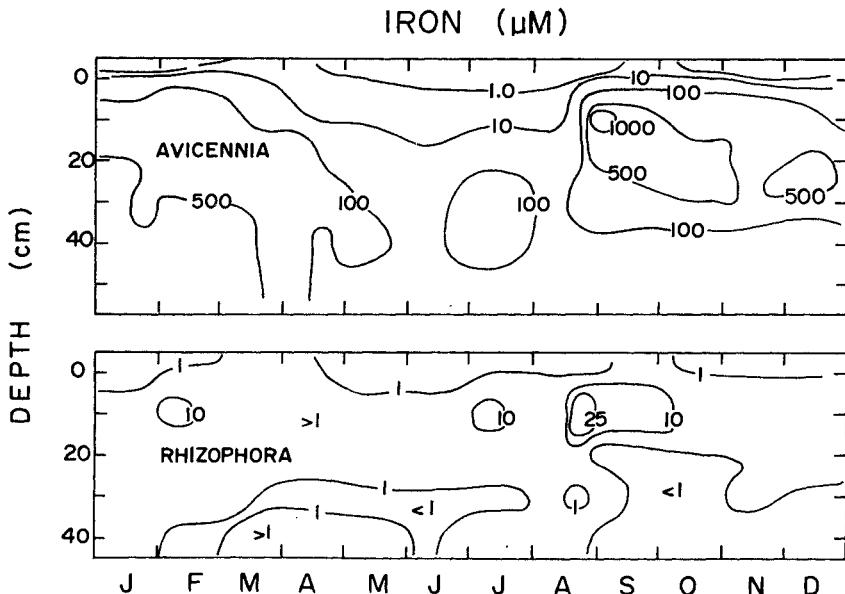


Figure 10.7: Pore water sulfide concentrations expressed as μ moles sulfide per liter pore water. Panels and sampling data as described for Figure 10.3



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Figure 10.8: Pore water iron concentrations expressed as μmoles dissolved iron per liter pore water. Panels and sampling data as described for Figure 10.3



other influences on sediment chemistry. Other potential bioturbative influences of the mangroves include supply of particulate and dissolved organic matter to the sediments, as well as differences in sulfate reduction rates and sulfide oxidation rates due to the flux of oxygen from the plant roots to the sediments. Marked differences in redox-sensitive parameters between the two zones could have been due to physical factors such as sedimentation rates, tidal inundation frequency, and pore water flushing rates. They might also have resulted from species-specific biological effects of the mangroves. Further investigation was required to determine whether the observed differences in redox-sensitive parameters were due to physical factors or biological factors.

EXPERIMENTAL STUDIES

Experimental studies to separate the effects of tidal inundation frequency from the bioturbative effects of the mangroves on redox-sensitive parameters were performed in impounded mangrove forests in the Indian River. Most of the mangrove communities along the east coast of Florida were impounded - enclosed by an earthen dike and flooded - in the early 1960s for saltmarsh mosquito control. The marshes are now flooded continuously from May to September and provide ideal experimental systems for the

separation of the effects of biological and physical factors on sediment chemistry.

Methods

Two impoundments were studied: C34, near Titusville, FL, which contains pure stands of Avicennia germinans, and HI5 near Fort Pierce, which is a pure stand of Rhizophora mangle. Both impoundments were closed and flooded in mid-May and reopened to tidal circulation in September. In the impoundments, ORP profiles were measured in the same manner as in the ISL site sediments. Pore water sulfide concentrations, however, were measured on depth-integrated samples, from the ground-water table to 30 cm. Pore water sulfide concentrations and sediment ORP values in the impoundments and in both zones of the ISL site were measured twice in 1984. Measurements were made first in August, when the ISL site was infrequently inundated and the impounded sites had been flooded continuously for three months. The second set of measurements was made in December, 1984, when the impounded sites were open to tidal circulation and tidal inundation frequency was frequent (but declining) after the fall maxima in both the natural and the impounded sites (cf. Figure 10.2).

During the summer of 1984, to test further the effects of mangroves on sediment chemistry, three PVC sleeves, 7.62 cm diameter and 30 cm long, were pushed into the sediments to the point that the cylinder tops were level with the mud surface in each zone of the ISL and C34 sites. These cylinders isolated a vertical column of sediment from the activity of roots while allowing any vertical movement of ground-water to continue unimpeded. Artifacts associated with root death in the cylinders were minimized by incubating the cylinders in situ for five months. Previous studies of root decomposition (e.g. Hackney and de la Cruz, 1980) have shown that bacteria respond rapidly to root death and readily oxidizable organic matter is consumed in less than four weeks. At the end of the experiment, redox profiles inside and outside the sleeve were measured with the stick electrode. Because the ORP electrode created a cylindrical hole 1 cm in diameter and 30 cm long inside the sleeve, each sleeve could only be sampled once.

Results

Mangrove sediment ORP values (Table 10.2) measured in August 1984, when the impoundment sites were flooded and the natural site was infrequently inundated, showed pronounced differences among sites reflecting the influence of both inundation patterns and differences of the two mangrove species on sediment chemistry. The natural Avicennia (ISL-AVI) zone sediments had the highest ORP values of all zones sampled, whereas the impounded Rhizophora (HI5) sediments had the lowest ORP values. The natural Rhizophora zone (ISL-RHI) sediments had higher ORP values than the impounded Avicennia (C34) sediments, demonstrating the large influence of inundation frequency on redox balance in the sediments. However, the difference between ORP values of impounded Avicennia (C34) and impounded Rhizophora (HI5) is

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probably due to a species-specific difference in the effects of the mangroves themselves on sediment chemistry.

Between August and December, inundation frequency and duration declined in the impoundments as they were opened to tidal exchange. During the same period, inundation at the natural site increased dramatically (cf. Figure 10.2). As a result, December ORP values showed a pattern which was different from August values, reflecting twice-daily tidal inundation and drainage at both natural and impounded sites. The ISL-AVI sediments still had significantly higher ORP values than other sediments, and HI5-AVI sediments were significantly more oxidized than ISL-RHI sediments which, in turn, were not significantly different from HI5-RHI sediments.

Sulfide concentrations (Table 10.3) mirrored ORP values in the sediments. During August, sulfide concentrations were undetectable in the natural Avicennia sediments and quite low in the natural Rhizophora and impounded Avicennia sediments. The highest concentrations occurred in the impounded Rhizophora sediments. In the December sampling, sulfide concentrations in the impounded Avicennia sediments had dropped, while they had risen in the natural Avicennia and Rhizophora sediments. Concentrations in the impounded Rhizophora sediments also increased slightly even though the impoundment was no longer constantly flooded.

Table 10.2: Oxidation-reduction potentials in natural and impounded mangrove sediments. All data are means of three replicate measurements at 10 cm depth in sediments. Data are not corrected for pH or temperature. Standard deviations are given in parentheses. Units are mV. Duncan multiple range test groupings indicated by letter subscripts. Values with the same letter are not significantly different ($a = 0.05$).

	<u>Avicennia</u> (C34) Impounded	<u>Avicennia</u> (ISL) Natural	<u>Rhizophora</u> (H15) Impounded	<u>Rhizophora</u> (ISL) Natural
August 1984				
-123 _c	109 _a		-349 _d	-38 _b
(34)	(17)		(16)	(16)
December 1984				
-217 _b	-174 _a		-318 _c	-315 _c
(40)	(16)		(20)	(14)

Table 10.3: Pore water sulfide concentrations in natural and impounded mangrove sediments. All data are means (standard deviation) of three replicate samples of depth-integrated pore water from 5 to 30 cm. Data are $\mu\text{mol/l}$. Values with the same subscript are not significantly different ($a = 0.05$)

	<u>Avicennia</u> (C34) Impounded	<u>ISL</u> Natural	<u>Rhizophora</u> (H15) Impounded	<u>ISL</u> Natural
August 1984				
21.5 _b (1.5)	dry -	480 _a (165)	8.6 _b (2.1)	
December 1984				
9.1 _b (1.7)	24.7 _b (12.9)	587 _a (257)	69 _b (39)	

ORP profiles of sediments inside and outside PVC sleeves (Table 10.4) clearly demonstrated the oxidative effects of the roots of both mangrove species on sediment chemistry. At every depth from 5 to 25 cm, ORP values of sediments isolated from roots within the PVC sleeves were significantly lower than values outside the sleeves for both species of mangroves. No sleeves were placed in impounded RHI sediments, but both natural and impounded Avicennia sediments showed a marked sleeve effect on ORP values. ORP values typically declined in the following sequence: ISL-AVI control > ISL-RHI control > C34-AVI control > H15-RHI control > ISL-AVI sleeve > C34-AVI sleeve > ISL-RHI sleeve.

Conclusions

On both sampling dates, ORP values were lower and sulfide concentrations were higher in the pore water of impounded sites than in natural sediments of both Rhizophora and Avicennia. From this we infer that inundation frequency and duration limit the penetration of oxygen into the sediments and, thus, influence pore water chemistry. Pore water sulfide concentrations in impounded Avicennia sediments were always lower and ORP values were always higher than in impounded Rhizophora sediments, and the pattern was the same for natural sediments, indicating that Avicennia and Rhizophora have different effects on sediment chemistry.

The sleeve experiments clearly show that the roots of both species of mangrove have oxidizing effects on sediments, raising ORP values and causing pore water sulfide concentrations to decline. Higher ORP values in both natural and impounded Avicennia sediments indicate that Avicennia has a greater capacity

Table 10.4: ORP values for natural and impounded Avicennia and Rhizophora sediments with and without sleeves. Each value represents a mean of three replicate readings. Data were collected 19-29 December 1984. No impounded Rhizophora sleeves were run

Depth grouping	Control	<u>Avicennia</u>			<u>Rhizophora</u>		
		Natural Sleeve	Control	Impounded Sleeve	Control	Natural Sleeve	Impounded Control
5	-126 a*	-283 c	-207 b	-299 c	-115 a	-303 c	-262 c
10	-116 a	-277 cd	-187 b	-312 cd	-123 a	-328 d	-265 c
15	-111 a	-267 b	-158 a	-319 bc	-142 a	-336 c	-267 b
20	-121 a	-254 b	-153 a	-320 bc	-179 a	-341 c	-273 b
25	-121 a	-254 c	-120 a	-307 cd	-197 b	-342 d	-281 c

Note: * Values with a particular grouping letter are not significantly different from values with the same depth according to Duncan's multiple range test with $\alpha=0.05$

to oxidize sediments than Rhizophora. Differences in sediment chemistry between Avicennia and Rhizophora zones cannot be attributed to differences in the amount or nature of organic matter, because ORP values in sleeved Avicennia sediments drop to levels similar to ORP values observed in Rhizophora sediments.

DISCUSSIONS

The sulfate:chlorinity ratios encountered in mangrove sediments far exceed values reported for field studies of temperate marsh sediments. Indeed, sulfate:chlorinity ratios in Spartina alterniflora sediments are typically depleted in sulfate because bacterial sulfate reduction rates are high (Howarth and Hobbie, 1982). Laboratory studies (McGovern et al., 1979; Carlson, 1980) indicate that Spartina may exclude sulfate to the same degree as Avicennia, but the bioturbative effect of transpiration is discernible in mangrove sediments because sulfate reduction rates and pore water turnover rates in Avicennia sediments are low and the biomass to sediment volume ratio in mangrove communities is extremely high.

Leakage of oxygen from roots of wetland plant species into the surrounding, typically anaerobic, sediments may have major impacts on sediment chemistry. Many wetland and aquatic plant species possess aerenchyma (air spaces), through which oxygen can diffuse from shoots to roots. When the capacity of the plant to supply oxygen to its roots exceeds the respiratory needs of root tissue, oxygen may diffuse out into the surrounding anaerobic sediments. Landmark papers by Laing (1940), Van Raalte (1941), and Scholander, Van Dam and Scholander (1955) reported root oxygen loss (ROL) for aquatic macrophytes, rice and mangroves, respectively. Teal and Kanwisher (1966) first reported ROL from Spartina alterniflora roots, and the phenomenon has since been 'rediscovered' in many other wetland and aquatic plant species (e.g. Dacey 1980).

Wetland sediment redox potentials depend on a variety of factors, such as the capacity of plants to leak oxygen to the sediments, the amount and degradability of organic matter in the sediments, and responses of the particular plant species to stresses such as hypoxia and potentially lethal pore water sulfide concentrations. Carlson (1980) reported that, despite its ability to live in highly reduced sediments, Spartina alterniflora does not have a large capacity to leak oxygen to the surrounding sediments. Measured ROL rates suggested that pore water sulfide could freely diffuse into the plant, and stable sulfur isotope ratio analyses of Spartina confirmed that sulfide was taken up and detoxified internally by Spartina (Carlson and Forrest, 1982). Although laboratory ROL rates for Spartina alterniflora are quite low, Howes, Howarth, Teal and Valielas (1981) have reported that Spartina has a pronounced oxidative effect on sediments and that sediment redox potentials are positively correlated with Spartina productivity. The oxidative effect of plants on the sediments may then be due in part to ROL, pore water turnover due to transpiration, and other, less well-understood factors such as bacterial symbionts (e.g. Joshi and Hollis, 1977). Oxygen loss from man-

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grove roots into the surrounding sediments probably inhibits obligate anaerobic sulfate-reducing bacteria, limiting sulfide production, or oxidizes sulfide as it is produced by bacteria, preventing the build-up of large amounts of reduced sulfur compounds in the sediments.

Whatever the mechanism involved, the capacity of Avicennia to oxidize sediments is quite large. We feel that conduction of oxygen through pneumatophores, specialized aerial roots, and ROL may comprise the major oxidative mechanism. Our results and conclusions agree to a large extent with those of Nickerson and Thibodeau (1985) and Thibodeau and Nickerson (1986) whose correlative and experimental studies also showed that Avicennia has an intense oxidizing effect on sediments. They found significantly lower redox potentials and higher sulfide concentrations in sediments without Avicennia roots than sediments with Avicennia present. They also found that sediment redox potentials decreased sharply when the tips of Avicennia pneumatophores were covered to prevent gas exchange. The sediment-oxidizing capacity of Avicennia is paradoxical when compared to the greater flooding tolerance of Rhizophora. The answer to the paradox is probably related to differences in root morphology between the two species and the fact that lenticels can develop adventitiously anywhere on a Rhizophora prop root, whereas the height of Avicennia pneumatophores is limited.

Thibodeau and Nickerson's (1986) experiments strongly suggest that the sediment-oxidizing capacity of Avicennia is due to ROL, and the history of mosquito control in the Indian River demonstrates that oxygen transport through pneumatophores is a critical factor limiting the flood tolerance of Avicennia. When the mangrove marshes of the Indian River were originally impounded for mosquito control, they were dominated by widely spaced Avicennia with large expanses of Batis maritima and Salicornia sp. (Harrington and Harrington, 1961). No attention was paid to flooding levels and virtually all of the impounded Avicennia died, apparently as the result of root anoxia. The impoundment C34, sampled in this study, was a demonstration project constructed in 1972 (Provost, 1973b). In one portion of the perimeter dike, the impoundment has a spillway graded to a level that allows water to spill out of the impoundment before the tips of Avicennia pneumatophores are flooded. Mosquito control is still achieved by flooding the marsh sediment surface to prevent oviposition by Aedes taeniorhynchus and Aedes sollicitans, and Avicennia trees have flourished over the past 14 years.

Our results indicate that Rhizophora also has a significant oxidative effect on the sediments, which differs from the conclusions of Thibodeau and Nickerson (1986). Whereas the apparent oxidative capacity of Rhizophora is not as great as that of Avicennia, sleeving Rhizophora sediments does cause significant declines in ORP values. Furthermore, we find that tidal inundation frequency also exerts a strong physical control on sediment chemistry. The study site of Thibodeau and Nickerson had no vertical zonation of mangroves; therefore they were unable to resolve differences in tidal inundation frequency between Rhizophora and Avicennia. Our results suggest that physical factors such as tidal

inundation frequency act in concert with the oxidative capacity of the mangroves to control sediment chemistry in areas where distinct vertical zonation of the mangroves occurs.

The species-specific differences in sediment-oxidizing capacity of Avicennia and Rhizophora which our data show may offer some insights on the problem of acid-sulfate soils on reclaimed mangrove sites. Flooded sediments with high sulfide concentrations frequently develop acid sulfate soils (with pH values less than 3.0) when they are drained and allowed to oxidize (cf. Dost, 1973). Acid sulfate soils on reclaimed mangrove sediments have been reported from Africa (Hart, 1959; Thornton and Giglioli, 1965; Hesse, 1961a, 1961b), Asia (Allbrook, 1973; Simpson, Ducklow, Deck and Cook, 1983), South America (Augustinus and Slager, 1971), and New Zealand (Dent, 1980) to cite but a few cases.

Pons (1973 and see Chapter 28) and Brinkman and Pons (1973) have extensively reviewed the occurrence of acid sulfate soils in reclaimed mangrove areas, and they suggest three guidelines for the prediction of acid sulfate soil development:

- (1) Mangrove sediments with high rates of organic sedimentation (i.e. peat formation) are likely to become acid upon oxidation.
- (2) Mangrove sediments with high rates of inorganic sedimentation (i.e. river deltas) are not as susceptible to acidification as are organic soils.
- (3) Partly as the result of (1) and (2) above, sediments dominated by Rhizophora are more prone to develop acid sulfate soils than are sediments where Avicennia dominates.

While most studies recognize that Rhizophora sediments are much more likely to develop acid sulfate soils than are Avicennia sediments, few if any acknowledge the active influence of the mangroves themselves on sediment chemistry. Most authors have concluded that higher organic matter production rates in mangrove sediments cause greater accumulation of reduced sulfur compounds. We suggest that, in the absence of cogent information on differences in the amount and degradability of organic matter in mangrove sediments, the observed differences in reduced sulfur compounds in Avicennia and Rhizophora sediments are due to higher tidal inundation frequency and lower root oxygen loss rates in Rhizophora sediments. Our data indicate that Avicennia may actively prevent the development of acid sulfate soils, while Rhizophora may actually enhance accumulation of reduced sulfur compounds which will generate acid sulfate soils on oxidation.

Our findings may be limited to areas of low tidal range such as the Indian River lagoon, where marked seasonal changes in tidal inundation frequency occur. In accord with the tidal energy subsidy hypothesis (Odum, Finn and Franz, 1979; Odum, Birch and Cooley, 1983), we might expect even higher sediment redox potentials and lower sulfide concentrations in areas with greater tidal ranges, and Boto and Wellington's (1983) study of mangrove sediment chemistry supports this hypothesis. They found that redox potentials and mangrove biomass declined significantly with increasing distance from tidal creeks and decreasing tidal inundation frequency. They attributed the declines to parallel decreases in

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the extractable phosphorus content of the soils, but pore water stagnation and the accumulation of sulfide and salt may also be responsible.

Although our results cannot be broadly applied to other systems, they do provide a nucleus for future studies. These studies should include test plantings of Avicennia seedlings in potential acid sulfate soils to test their capacity to oxidize reduced sediments and further studies of pore water chemistry in mangrove forests with high and low tidal energy regimes.

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Chapter Eleven

THE VALUE OF WETLANDS IN LOW RELIEF LANDSCAPES

M.T. Brown and M.F. Sullivan

INTRODUCTION

Much is known about wetland values, especially the values of wetlands associated with water bodies and stream corridors. A great deal of work has been done and is still being done concerning the value of coastal marshes and swamps to estuarine productivity and the values associated with floodplain wetlands and bottomland hardwood ecosystems. Values are associated with wildlife utilization and support and water quality functions among others. While much is known about wetland values, it still remains almost impossible to assess their values to society and therefore quantitatively to answer questions of public policy.

In general, wetlands are well protected and much public awareness has been directed toward their effective management. However, little attention and even less public awareness concerning the values of 'isolated' wetlands such as marshes, bayheads, and cypress domes found in the low relief landscapes like that of central Florida has been fostered in recent years. These headwater wetlands are confined to a few areas within the country and to relatively unrecognized positions of importance within the landscape.

Because of their landscape position, few regulations can exert effective protection over isolated wetlands, and yet, by their very location as the headwaters of most streams and rivers in low relief landscapes, their protection is vital for maintenance of downstream water quality and quantity. Isolated wetlands in low relief landscapes, like those characteristic of the southern coastal plain, play a particularly important role in maintaining high ground waters, base flow of streams, and good water quality as well as wildlife habitat and increased landscape diversity.

The Need for Establishing Wetland Values

The term isolated wetlands has come into use to describe those wetlands that are not hydraulically connected to flowing waters. In Florida where recent legislation has defined wetlands as waters of the state and thus worthy of protection, isolated wetlands by virtue of their non-connected status, do not fall under state protection. Other regional agencies (Water Management Districts)

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have some regulatory powers over isolated wetlands under surface water management rules. At the present time, however, there is much controversy over the minimum size of isolated wetlands that should fall under these rules. Legislation has just been passed that will set the minimum size at approximately two hectares and require agencies to develop a methodology to determine the value of any wetland so that a benefit/cost ratio may be calculated for any proposed development action. With a standard methodology, agencies may determine if the benefit of developing a wetland will exceed the value of keeping the wetland intact.

Whereas the intent of the legislators may have been to establish a predictable system by which wetland values may be determined and weighed against the benefits to society of destroying them, past methodologies have not lent themselves to such economic manipulations (see Winchester, 1982; Adamus and Stockwell, 1983; Brown and Starnes, 1983). Most have been developed to weigh one wetland against another and decide questions of ranking. The results are often qualitative, determining a ranking on such measures as size, intactness, wildlife use, life form richness, etc.

The question still remains. How valuable are wetlands? Are they more valuable than another land use that may occupy the same place in the landscape, such as housing, industry, or commercial development?

A different, but related area of intense interest is mitigation of wetland impacts and losses. The uses of mitigation in some instances are as punitive measures, and in others as a means of allowing flexibility in developing the landscape if wetland losses that may result are somehow mitigated. The mitigation can take several forms: reconstruction, enhancement, monetary payment, or combinations of these. The question that still must be answered, however, once the public accepts the concept of mitigation, is what is the worth of the values that are impacted and that are being mitigated? Any system of mitigation must address this question or otherwise stab blindly at managing the landscape.

In this chapter characteristics and functions of wetlands are explored, their position in low relief landscapes explained, and various values and a technique for estimating and comparing them are determined. A macroscopic minimodel of watershed hydrology is simulated to show different patterns of runoff hydrographs with and without wetlands in the landscape, and landscape management alternatives that maximize wetland values and economic use are suggested.

WETLANDS IN LOW RELIEF LANDSCAPES

In the very flat landscapes like those characteristic of the southern coastal plain, the organization of drainage networks is somewhat different from that found in higher relief basins. Headwater areas are larger, channelways smaller, and distributions of isolated wetlands and those connected to river courses are different. Figures 11.1 and 11.2 show maps of typical water basins, the first a high relief basin and the second a low relief basin. The pie charts with each show the relative amounts of

channelway vs. headwater area, and the amount of wetlands within each. In high relief basins, wetlands are most commonly associated with the river floodplain, while in lower relief basins, most wetlands are not associated with the floodplain, but occur as isolated systems in the headwaters and far reaches of the channelways. These data are based on studies of over 30 basins in north central Florida and represent mean areas of wetlands, headwaters and channelways.

In low relief watersheds, headwater areas are between 30 and 50 per cent of the total area, wetlands are often greater than 30 per cent of total area, and isolated wetlands comprise the majority of wetland area. By comparison, high relief landscapes have minimal headwater areas, wetlands are usually less than 10 per cent of total area, and isolated wetlands are a minor component of the landscape, where riverine (or floodplain) wetlands are the most common type.

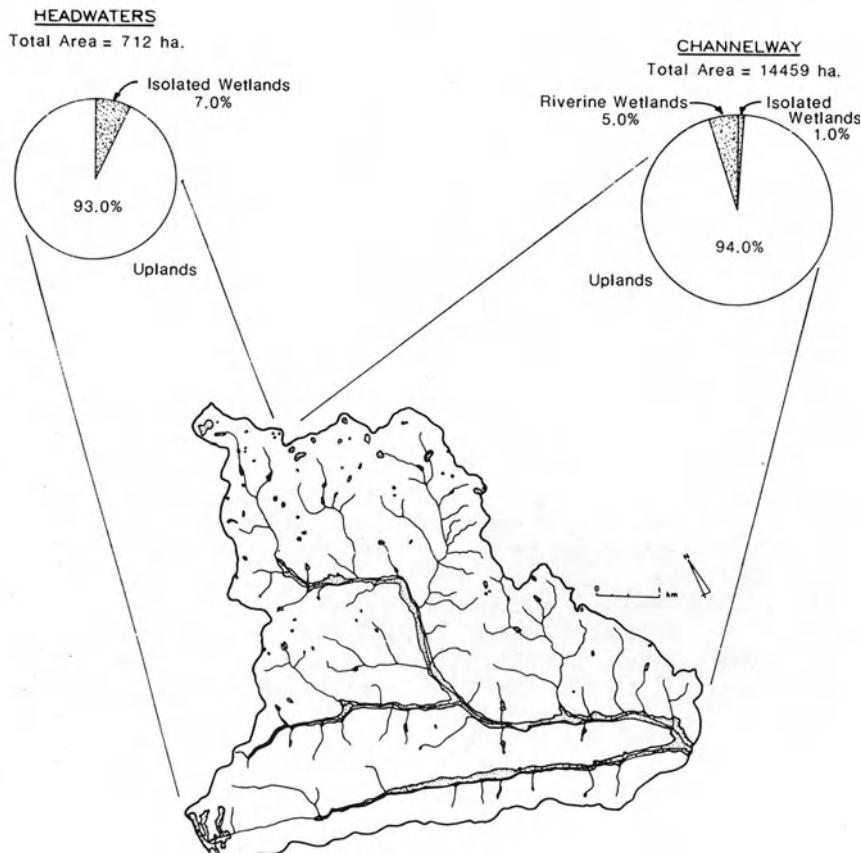
Management strategies for these different watersheds should reflect the differences in overall organization. Regulations that protect water quality through restrictions on dredging and filling floodplain wetlands are important in high relief landscapes where floodplain swamps are the dominant wetland type, but will have minor impact if implemented in low relief landscapes. Because isolated wetlands, by definition, are not hydraulically connected to surface waters, their value is not in direct contributions to the quality of these waters, but in storage and maintenance of quality of ground waters. Watersheds with large areas of wetlands have more uniform surface discharge and have more constant baseflow as a result of wetland storage.

The size class distribution of isolated wetlands in low relief landscapes as shown in Figure 11.3(a) reveals a hierarchy of size classes. These data are the cumulative totals for 32 basins in north central Florida. Generally, value as wildlife habitat and contribution to species richness is held to increase with increasing size of 'island' based on relationships demonstrated with species area curves (Arrhenius, 1921; Gleason, 1922; Preston, 1960, 1962). However, when the number of individual isolated wetlands as shown in Figure 11.3 is factored in, the total number of individuals that may be affected with declines in the abundance of small isolated wetlands may be significant. The effects may be greater than the loss of one large wetland of comparable acreage, since gene pools, breeding potential, and ultimately community stability may be affected (Odum, Cantlon and Kornicker, 1960).

Figure 11.3(b) shows the percentage of total wetland area in each of the five size classes within the 32 watersheds. The notion that small wetlands may not be important because they represent a small portion of the total area of wetlands is not upheld by these data. The size classes of less than 4.0 hectares make up almost 15 per cent of total wetland area.

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Figure 11.1: Map of a typical high relief watershed. Stippled areas are wetlands. Pie diagrams show the percentage wetlands and total area in headwater and channelway. In high relief watersheds, area of wetlands is a minor component of the landscape, and in the channelway, riverine wetlands predominate



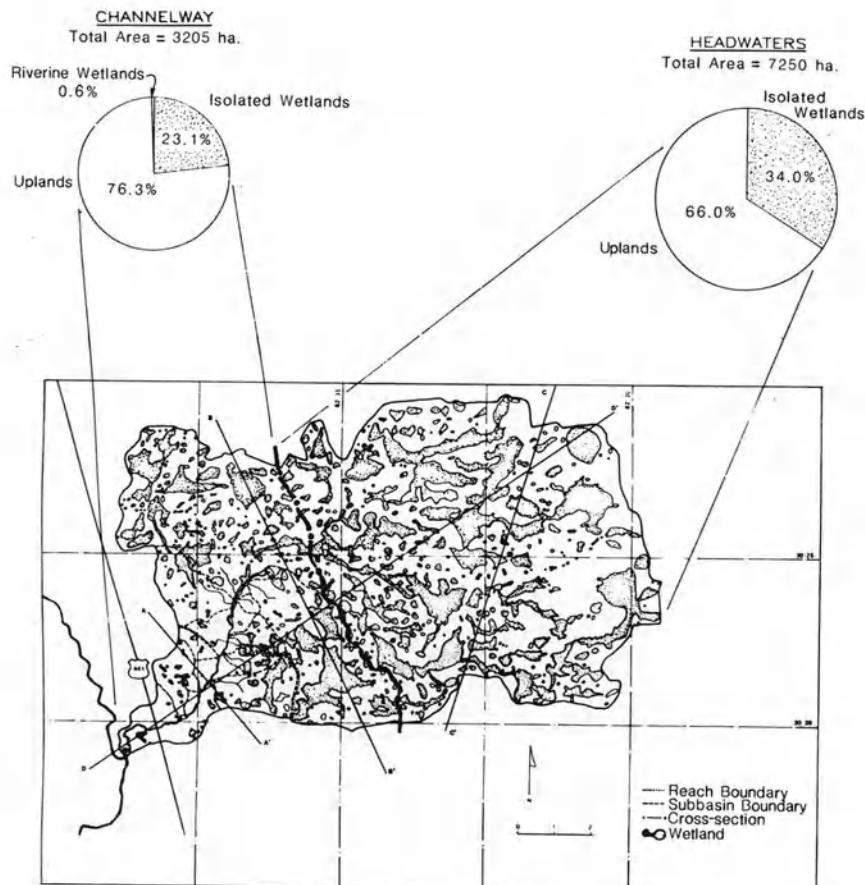
Source: Data and map from Sullivan (1986)

WETLAND VALUES

Simulating Hydrological Values

Values associated with wetlands include hydrological values like flood attenuation and water storage, among others. Water stored in wetlands is held on the landscape and used to maintain higher ground-water levels. At the same time, wetland storage helps to reduce flood peaks in downstream channels and maintain dry season baseflow. To better understand these relationships (and since it is nearly impossible to find paired watersheds, with and

Figure 11.2: Map of a typical low relief watershed. Stippled areas are wetlands. Pie diagrams show the percentage wetlands and total area in headwaters and channelway. The headwaters comprise over 60% of the total basin area, isolated wetlands are approximately 30% of total area, and riverine wetlands are a minor component of the landscape



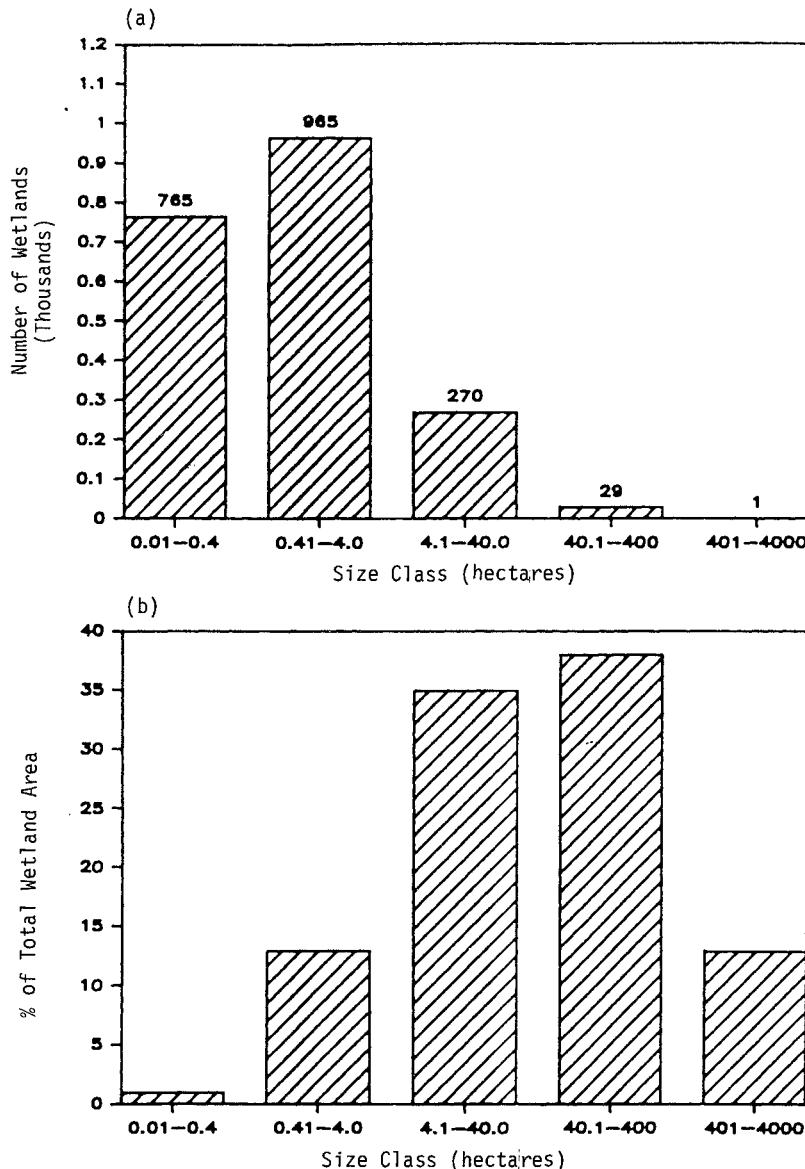
Source: Data and map from Sullivan (1986)

without wetlands), simple macroscopic minimodels of watersheds with and without wetlands can be simulated on computer and temporal hydrologic behavior observed.

Macroscopic minimodels (Odum, 1976) are a class of simulation model where the complexity of the real world is simplified, retaining necessary components and relationships, to perceive macroscopic behavior without overwhelming the user with a complex 'blackbox' program. They are termed minimodels because they are

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Figure 11.3: Size frequency graph of wetlands in 30 low relief watersheds in northcentral Florida (a) and percentage of total wetland area by size class (b). Wetlands less than 4 hectares comprise 83% of the total number of wetlands and approximately 15% of total area



Source: Data from Sullivan (1986)

small enough and simple enough for the user to be able to identify all components, pathways, and processes and understand how the model functions.

The diagram in Figure 11.4 is an energy circuit diagram of a simulation model for a typical low relief watershed. Forcing functions include rainfall, sunlight driving evaporation and transpiration, and inflowing ground water. Storages of water within the watershed include wetland storage, surface water in streams and river, and shallow ground water. Additional variables used in the simulation are watershed area and wetland area. The model is programmed in BASIC and simulated on a desk-top micro-computer. Numbers in the diagram are average yearly flows and storages of water in the watershed. The inflow of shallow ground water is assumed to be equal to outflow and is therefore not accounted for in the model.

Simulation results are shown in Figure 11.5 for two conditions: the first where there are no wetlands within the watershed, and the second where 30 per cent of the watershed is composed of wetlands. The most striking difference is the lower overall discharge and the attenuation of flood peaks in the second graph representing the condition of 30 per cent wetlands in the watershed. In addition, ground waters do not fluctuate as much and remain higher throughout the year.

Macroeconomic Values of Wetlands

Increasingly, public policy requires that the values of natural ecological systems be compared with values generated as a result of economic interaction. Such comparison is usually done as some form of benefit/cost analysis. However, since the processes and functions of natural systems always fall outside the monetized economy, there is no equitable way of establishing value for services like wildlife habitat, gross primary production, or ground-water recharge. Willingness to pay is not an equitable argument, since having never paid for gross primary production, for example, one does not perceive its true value.

Techniques of energy analysis use the energy values of processes and storages of resources to determine contribution to the economy (see Gilliland, 1978; Odum, 1978, 1984; Odum, Lavine, Wang, Miller, Alexander and Bukler, 1983). Energy values are converted into macroeconomic value - a dollar measure of the process or resource contribution. In this way, the value of natural systems and their processes can be compared on an equivalent basis with systems and processes dominated by humanity and a dollar value can be assigned.

Table 11.1 gives an energy analysis of some functions and storages of one acre of cypress wetlands in northcentral Florida. In the second column each item is listed. In column 3 their energy value, then their transformity, solar energy (spelled with an 'm' and abbreviated as *sej*) and macroeconomic value in columns 4 through 6. In the first column a footnote number is given as reference to calculations that follow the table.

The method of energy analysis is first to calculate the energy value of the storage or flux (column 3), then to multiply by the

Figure 11.4: Energy circuit diagram of the watershed hydrology model showing the driving energies of rainfall, sunlight, and groundwater inflow, and storages of land, water in wetlands, surface water and ground water. Equations and computer program in BASIC are available from the authors

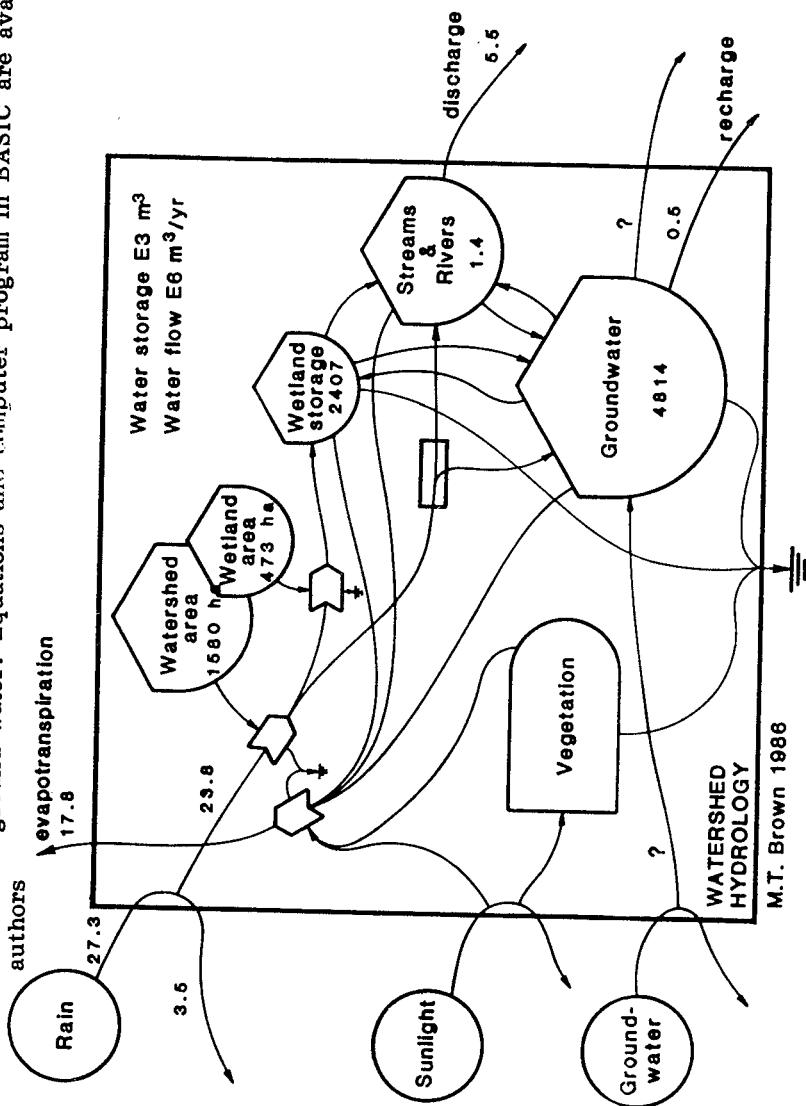
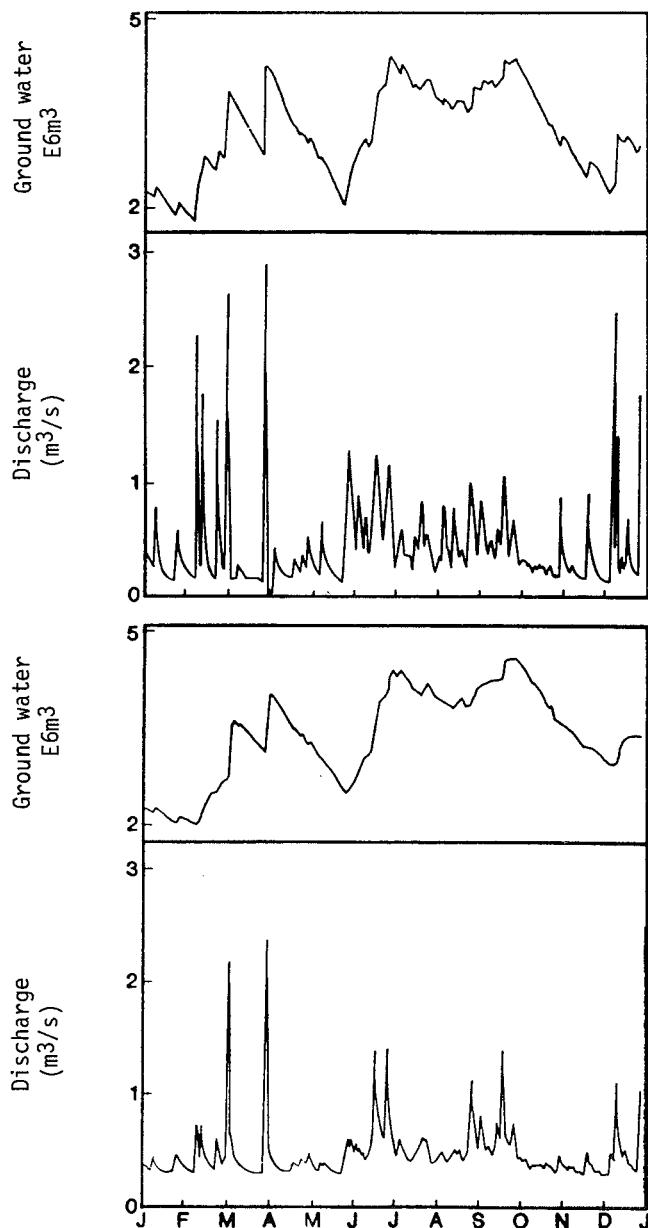


Figure 11.5: Simulation results of the model in Figure 11.4 showing ground water elevations and discharge hydrograph for a watershed with no wetlands in the top graph, and for a watershed with 30% of land area in wetlands in the bottom graph



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Table 11.1: Values of functions and storages of 1 acre of cypress wetlands in northcentral Florida

Footnote	Item	Energy value (E12 joules)	Transformity ^a (sej/joule)	Solar emergy ^b (E15 sej)	Macro- economic value ^c (1983 US\$)
Market values					
1.	Land	-	-	-	2,500
2.	Wood	-	-	-	12,000
Long-term storages					
3.	Wood	1.5	3.0 E4	45.0	18,750
4.	Peat	6.8	3.5 E4	238.0	99,160
5.	Water	0.02	4.1 E4	0.82	340
Yearly flux					
6.	Gross primary production	0.15	1.5 E4	2.25	940
7.	Water recharge	0.009	4.5 E4	0.4	170

Notes: a, Transformity is the solar emergy per unit of energy.
 Solar transformity of an item is the solar emergy required to generate that item efficiently and rapidly.
 Transformities are an energy-based natural scale of value.
 b, Solar emergy (spelled with an 'm') is obtained by multiplying the actual energy of an item by its transformity. It is a common measure of value which is the solar energy required to generate the resource.
 c, Macroeconomic value is obtained by multiplying solar emergy in column 5 by the emergy/dollar ratio for the US economy. The emergy/dollar ratio for the US is the ratio of the total emergy used by the country from all sources divided by the gross national product for that year. In 1983, the US emergy/dollar ratio was 2.4 E12 sej/\$.

Footnotes to Table 11.1

- Real estate value based on recent sales information supplied by Gainesville, Florida, based realtors.
- Market value of wood based on estimated dollar value of end product of \$3.00/bd ft and assuming 4,000 bd ft per acre.
- Standing crop of marketable wood taken as 25 kg/m² (Brown, 1978)

$$\begin{aligned}
 \text{Energy value} &= (25,000 \text{ g/m}^2) (4,047 \text{ m}^2/\text{acre}) (3.5 \\
 &\quad \text{Cal/g}) (4,186 \text{ J/Cal}) \\
 &= 1.5 \text{ E12 J/acre}
 \end{aligned}$$

4. Average peat depth estimated from 12 cypress domes of north central Florida as 0.75 m

$$\text{Total volume} = (0.75 \text{ m}) (4,047 \text{ m}^2/\text{acre}) = 3.04 \text{ E3 m}^3$$

$$\text{Dry weight} = 10.4\%; \text{ heat content} = 5.1 \text{ Cal/g dry wt.}$$

$$\begin{aligned}\text{Total peat} &= (3.04 \text{ E3 m}^3) (1 \text{ E6 g/m}^3) (0.104\% \text{ dry wt}) \\ &= 3.16 \text{ E8 g dry wt/acre}\end{aligned}$$

$$\begin{aligned}\text{Energy value} &= (3.16 \text{ E8 g}) (5.1 \text{ Cal/g}) (4,186 \text{ J/Cal}) \\ &= 6.8 \text{ E12 J/acre}\end{aligned}$$

5. Volume of water held in swamp equal to average sun/acre storage (av. depth 30 cm), plus water held in peat (89.6% moisture).

$$\text{Surface water} = (0.3 \text{ m}) (4,047 \text{ m}^2/\text{acre}) = 1.2 \text{ E3 m}^3$$

$$\begin{aligned}\text{Peat water} &= (3.04 \text{ E3 m}^3 \text{ peat}) (89.6\% \text{ water}) = 2.7 \text{ E3 m}^3 \\ \text{Total water} &= 3.9 \text{ E3 m}^3\end{aligned}$$

$$\text{Gibbs free energy of soft water} = 5 \text{ joules/g}$$

$$\begin{aligned}\text{Energy value} &= (3.9 \text{ E3 m}^3) (1 \text{ E6 g/m}^3) (5 \text{ joules/g}) = \\ &1.95 \text{ E10}\end{aligned}$$

6. Annual value of swamp work is determined using transpiration of cypress as a measure of primary production. Water use was taken as 1,775 g H₂O/g CH₂O, and average GPP of 7.9 g C/m² day⁻¹ and 30 g CH₂O per 12 g carbon.

$$\begin{aligned}\text{Yearly water use} &= (7.9 \text{ g C/m}^2 \text{ day}^{-1}) (214 \text{ days}) (30/12) \\ &\quad (1,775 \text{ g H}_2\text{O/g CH}_2\text{O}) (4,047 \text{ m}^2/\text{acre}) \\ &= 3.03 \text{ E10 g H}_2\text{O/acre yr}^{-1}\end{aligned}$$

$$\begin{aligned}\text{Energy value} &= (3.03 \text{ E10 g H}_2\text{O}) (5 \text{ joules/g}) \\ &= 1.5 \text{ E11 J/acre yr}^{-1}\end{aligned}$$

7. Recharge taken as 45 cm/yr

$$\begin{aligned}\text{Water recharged} &= (45 \text{ cm/yr}) (4,047) (1 \text{ E4 cm}^2/\text{m}^2) \\ &\quad (1 \text{ g/cm}^3) \\ &= 1.8 \text{ E9 g/yr}\end{aligned}$$

$$\text{Energy value} = (1.8 \text{ E9 g/yr}) (5 \text{ J/g}) = 9 \text{ E9 J/yr}$$

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appropriate transformity (see Odum, 1986), resulting in solar energy (column 5), and then to multiply by an energy/dollar ratio for the economy to obtain macroeconomic value (column 6). Dollar values obtained can be used to evaluate the costs and benefits when development of wetlands is proposed, appropriate monetary mitigation, or maximum investments in reclamation activities. It is probably not appropriate to add values for storages in column 6 together, since the ecosystem is a web of energy flows, and double counting would result. Generally, the highest value obtained for storages in the energy analysis is used.

The macroeconomic value of yearly fluxes, like items 6 and 7, may be an appropriate measure to estimate the yearly contribution of the ecosystem to the economy and therefore a means of determining value on a recurring basis. These values may be added together since they result from the chemical potential energy in water, as water transpired and recharged. The combined total is over \$1,100/acre yr⁻¹.

Summarizing Wetland Values

Data from spatial analysis suggest that isolated wetlands are an important component of low relief landscapes requiring special regulation since their chief values are not related directly to water quality of flowing surface waters. Size class distributions and percentage of wetland area in small wetlands show the importance of wetlands less than 4 hectares. Computer simulation of macroscopic minimodels of watershed hydrology indicates that increasing wetland area within watersheds reduces peak floods and increases ground-water levels. Energy analysis of storages and fluxes in wetland ecosystems shows high macroeconomic values for comparison with economic activities and can be used to evaluate mitigation and reclamation plans.

ACKNOWLEDGMENT

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Chapter Twelve

WETLAND EVAPOTRANSPIRATION IN TEMPERATE AND ARID CLIMATES

R.H. Kadlec, R.B. Williams and R.D. Scheffe

INTRODUCTION

Water losses to the atmosphere from wetlands are a combination of evaporation and transpiration by emergent macrophytes. Wetland surfaces may be permanently or periodically saturated, with periods of shallow standing water. A variable fraction of the surface area may be occupied by open water. The soil surface may be bare or covered by a litter layer that forms an effective mulch.

This complexity would appear to lead to widely disparate water losses, but in fact does not. Two factors cause a narrow range of values: (a) the source of vaporization energy is the sun; and (b) wetlands that are normally saturated are capable of realizing their full evaporation potential. Meteorological factors that modify the use of solar energy for vaporization are well known: wind, relative humidity, temperature and cloud cover.

The water budget for a wetland provides the framework for understanding and interpreting all other wetland functions. Evapotranspiration, together with streamflow and ground-water recharge, are the only possible water removal processes. Both sites in this study were impacted by treated wastewater additions, and hence water quality was of primary importance. Knowledge of the water budget was necessary to correlate observations of water quality and ecosystem response.

Transpiration denotes water losses to the atmosphere from the vegetation, whereas evaporation refers to water losses from the soil and water surfaces. In combination, these are termed evapotranspiration, and all are on an areal basis. Pan evaporation refers to losses from containers of various sizes in various environments.

The ultimate goal was the prediction of evapotranspiration from site characteristics and environmental factors. Hence, several equations were tested for precision, accuracy and site specificity.

The Houghton Lake, Michigan site, located in the central lower peninsula, is a flow-through wetland, with complete vegetation cover. The water table fluctuates from spring high water (depth about 25 cm) to summer low water (dry to 5 cm). The two dominant cover types were 950 ha of sedge willow (*Carex* spp. and *Salix* spp.) and 140 ha of leatherleaf-bog birch (*Chamaedaphne calyculata* and *Betula pumila*). There were lesser amounts of cattail (*Typha* spp.) (13 ha) and alder edges (*Alnus rugosa*) (24 ha).

Further descriptions may be found in Wentz (1976) and Chamie (1975).

The Carson City, NV site is a constructed, zero-discharge wetland, consisting of 21 interconnected cells fed with secondary wastewater from Incline Village. Water depths vary seasonally from dry to about 60 cm. It is adjacent to a natural wetland, fed by hot springs, where water exists year round in ponds and channels at depths up to one meter. Warm water exits through two of the constructed cells to the Carson River. This natural wetland consists of three major cover types: rush meadows (*Juncus balticus*), threesquare bulrush (*Scirpus americanus*), and tule-cattail (*Scirpus acutus* and *Typha latifolia*). The constructed wetland sites were originally occupied by sagebrush (*Artemesia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), greasewood (*Sarcobatus vermiculatus*), and saltgrass (*Distichlis spicata*). Sixteen cells had this vegetation removed, while the remainder were flooded in their original state. Further details may be found in CH2M-Hill (1980) and Culp, Wesner, Culp (1986).

METHODS

Houghton Lake

Pan evaporation data were obtained in several vegetation types using USWB Class A and smaller pans from 1976 through 1979. Measurements of water level change were periodically taken to the nearest millimeter. Water levels were also measured in planted lysimeters (garbage cans). Evapotranspiration data for 1976-9 were acquired from water level recorders placed in several locations. Evapotranspiration was determined from day/night loss differentials (Heimburg, 1977). A small amount of data was obtained from a microcosm evaporimeter in 1977. A clear, plastic box, approximately 0.5 meter on each edge and open on one side, was equipped with a vapor flow meter. This was placed over vegetation with water, forming a vapor seal around the lower edge. The flowmeter was immediately placed in the outlet hole, and readings were taken every 15 seconds for three minutes. After a brief induction period, vapor flow reached a slowly declining state.

During 1976, Scheffe (1978) determined direct transpiration from willow, bog birch, leatherleaf and sedge. A branch was enclosed in a chamber, with air flow and humidities measured, allowing calculation of transpiration by mass balance.

Solar radiation, air temperature, relative humidity and wind speed were recorded at the wetland site and adjacent locations. A recording pyranograph, a recording hygrothermograph, and a recording anemometer were used at an adjacent upland site, together with similar data from a nearby NOAA weather station (Houghton Lake Porter Ranch).

Piche atmometers, consisting of graduated water-filled tubes with wicks, were suspended at 0.5 and 1.5 meters above ground in a wetland edge site. Daily readings to the nearest 0.01 mm were taken from May through August in 1974 and 1975.

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Carson City

Several types of data were collected, primarily during the spring-summer season, during which most water losses occur. Two weather stations were established at the wetlands: an evaporation station near the first constructed wetlands cell, and a climatological station near the operations building (Weather Bureau, 1970). The evaporation station consisted of a Class A pan with a level recorder, a hook gauge, and Six's thermometer: a precipitation gauge: and a anemometer. The climatological station was equipped with a recording pyranograph, a recording hygrothermograph, a recording barometer, a recording precipitation gauge, a recording anemometer, and a maximum/minimum thermometer.

Each of the first 16 wetlands cells was equipped with a staff gauge, and could be isolated by use of high weir plates. During June and July 1985, these cells were isolated so that effluent did not enter or leave them. Cell 8 was isolated similarly during June and early July, and was equipped with a level recorder. Level measurements in these cells were used to determine evaporation from the wetlands cells, and these were compared to the pan evaporation rates.

Since 1985, there was no significant amount of vegetation in any cell containing water and measuring equipment. Readings were taken and charts were changed on a weekly basis, with more frequent readings during periods when staff were at the site daily. In particular, diurnal variations were monitored on two occasions. Electrical conductivity of the water in the cells was measured in June and July 1985, providing a rough check on evaporation by material balance.

Daily water loss values were determined from level recordings. Weekly values were obtained from staff gauges and the hook gauge. In Table 12.6 these are given as monthly totals. Because of ice formation in the Class A pan, data could be obtained only from late March until mid-November, at which time temperatures dropped to below zero Fahrenheit for several days, causing thick ice formation. Evaporation data were not collected during late August and early September, when field assistance was unavailable. As a result, daily evaporation values were obtained for 178 days. Levels were monitored during June and July for 15 cells, using staff gauges, and for Cell 8 using a level recorder during June.

RESULTS AND DISCUSSION

Houghton Lake

Evaporation from bare peat and from litter-covered peat are less than pan evaporation (Table 12.1). In fact, water loss from litter covered areas is very small, as might be expected. Since most of the wetland surface is so covered, evaporation from saturated, non-inundated areas appears to be negligible.

There are significant losses when the litter layer is covered by water. Table 12.2 gives pan evaporation from open and shaded areas, together with evapotranspiration from the same localities. Free surface (pan) evaporation is strongly influenced by shading, which is dependent on cover type. The cover types order as

Table 12.1: Results of field studies of evaporation from exposed peat and water

		Evaporation (mm/day)
H ₂ O Class A pan	Sedge site 480 cal/cm ² day	6 ± 3
Peat	Sedge site 480 cal/cm ² day	4 ± 1
Peat, litter-covered	Sedge site 380 cal/cm ² day	0.1 ± 0.1

anticipated, except for alder, which provides more shade than sedge. The greatest loss is from the most open cover (meadow), the least from the most dense (leatherleaf). Some of the effect is due to wind and humidity differences, as indicated by the 1979 data from pans placed in unshaded areas. Data for evapotranspiration show much reduced variation with cover type (Table 12.2, Evapotranspiration). The transpiration component apparently uses the radiation blocked from the evaporative surface.

Data in Table 12.3 further illustrate the cover type differences in pan evaporation and evapotranspiration, with potted plant level changes also given. The high level changes reflect the water-holding capacity of the peat soil for the potted plants: the below-surface water is selectively 'wicked' away from the measurement well, causing false water loss measurements.

Vapor flows from the microcosm chamber are shown in Figure 12.1. Vapor flow from the chamber changes during an initial induction period of about 30 s, representing the chamber capacity transient. The subsequent slow decrease represents the alteration of climatic conditions within the chamber. This response is linear, and hence may be extrapolated to the starting time, at which normal conditions prevailed. The diurnal variation is clearly shown by the progression of intercepts through the day.

Daily and weekly values of evapotranspiration from a sedge site are shown in Figures 12.2 and 12.3, respectively. It is clear that daily values fluctuate about ± 25 per cent from the mean seasonal curve. This is in response to variations in the environmental factors that drive evapotranspiration - sunshine, wind, humidity and temperature.

Transpiration data for one diurnal cycle for sedge are shown in Figure 12.4. Hour-to-hour variations are also approximately ± 25 per cent. Such species transpiration measurements may be combined with standing crop data to estimate areal transpiration (Table 12.4). Estimates are high for sedge-willow and low for leatherleaf-bogbirch, probably due to the variability of standing crop from plot to plot. Furthermore, the mosses under the leatherleaf have not been included.

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Table 12.2: Effects of cover type and shading on June pan evaporation and evapotranspiration (mm/day)

	Meadow	Sedge	Cattail	Pan Leatherleaf	Alder
1976	6.20	5.50	4.85	3.50	4.60
1979 open	5.54	2.83	3.83	3.60	-
1979 shaded	-	1.83	2.33	1.33	-
Evapotranspiration					
1976		4.75		4.58	
1978		4.08		-	

Table 12.3: Water level changes in wells, field data

		Evaporative level change (mm/day)
Wide, shallow well Stevens recorder	Sedge site Summer average	4.7 ± 1.1
Shallow narrow well, uncased potted sedge	Sedge site Summer average	14.0 ± 5.0
Shallow narrow well, uncased potted cattail	Cattail site Summer average	10.0 ± 1.0
Shallow narrow well, uncased potted leatherleaf	Leatherleaf site Summer average	13.0 ± 3.0
Class A Pan	Sedge site Summer average	4.6 ± 1.0
Class A Pan	Cattail site Summer average	3.9 ± 0.7
Class A Pan	Leatherleaf site Summer average	3.3 ± 0.5

Figure 12.1: Microcosm chamber evapotranspiration versus time

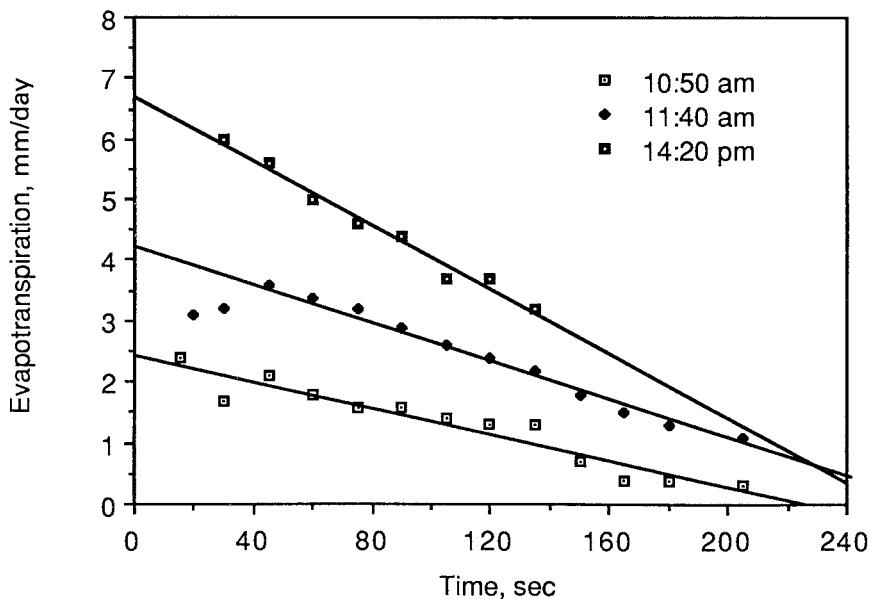
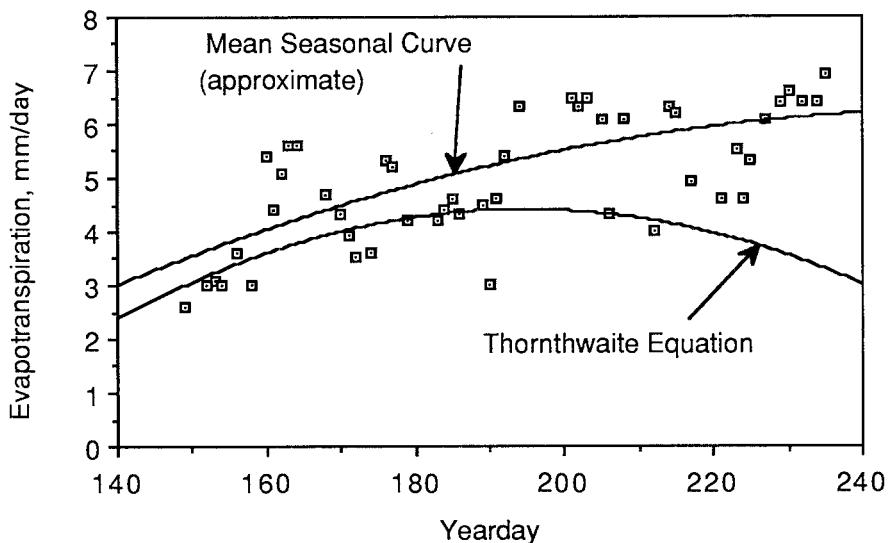


Figure 12.2: Houghton Lake evapotranspiration, sedge site, 1977



HYDROLOGIC & WATER QUALITY VALUES OF WETLANDS

Figure 12.3: Comparison of evapotranspiration and pan evaporation (sedge site, Houghton Lake, 1976)

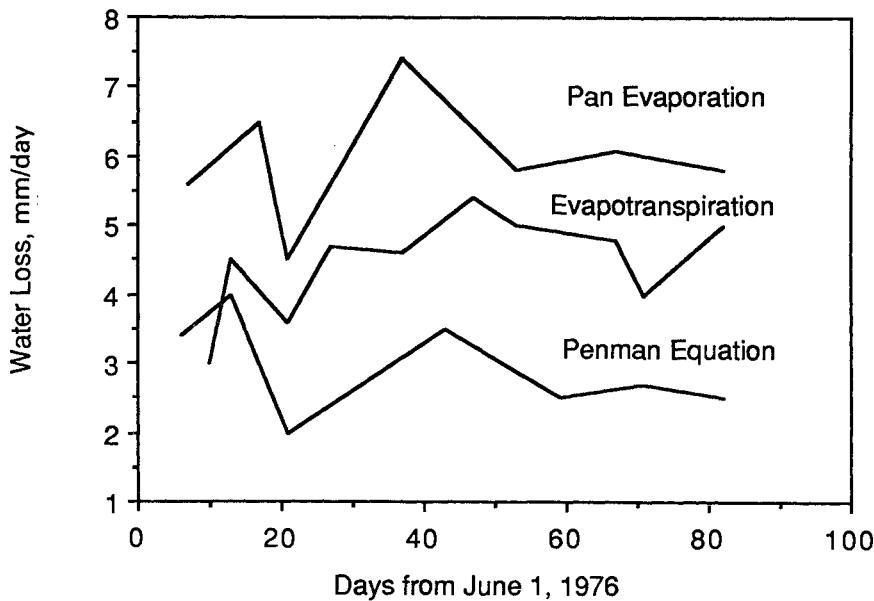
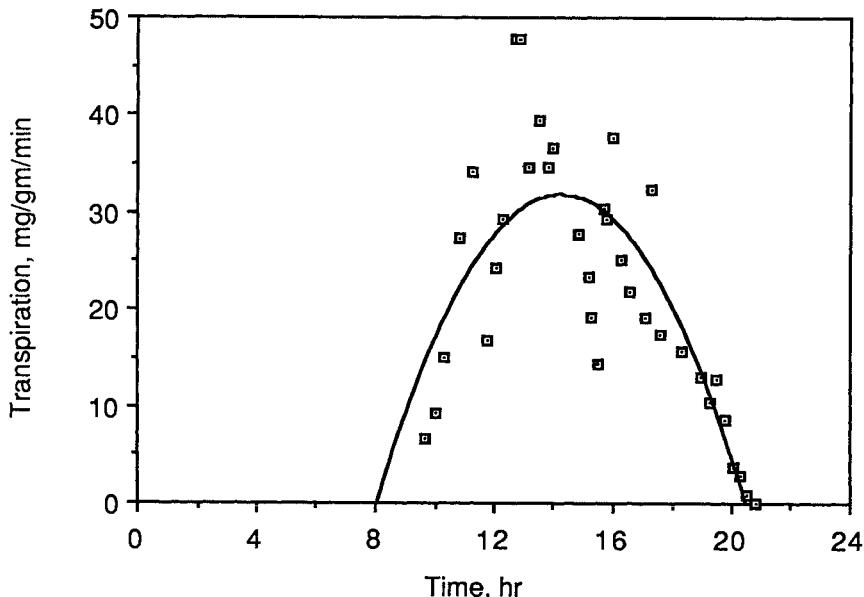


Figure 12.4: Diurnal variation of sedge transpiration, 19-21 August 1976



Source: From Scheffe (1978)

Table 12.4: Effect of cover type on transpiration

Species	Water loss		Cover type ^a		
	g/g day ⁻¹	g/m ²	SW mm/day	LL-BB g/m ²	LL-BB mm/day
Sedge	26.4	225	6.0	20	0.5
Willow	22.9	31	0.7	—	—
Bogbirch	21.6	—	—	57	1.2
Leatherleaf	12.7	—	—	107	1.4
Total		256	6.7	184	3.1

Note: a, SW = sedge-willow; LL-BB = leatherleaf bogbirch

Source: Scheffe (1978)

The Piche atmometers gave low and inconsistent results, and will not be discussed further.

Carson City

The climatological factors are summarized in Table 12.5. The area is characterized by moderate to average temperatures and low relative humidity (35 per cent annual average in 1985). Relative humidity was determined as the daytime average value from the chart records. Solar radiation is high: the values shown represent 87 per cent of the maximum, as determined from pyranograph records on cloudless days. There are some differences between measured radiation and that given in the literature for this latitude (Christiansen and Low, 1970). This difference is probably due to the shading effect of mountains to the east and west.

Strong winds in late afternoon in summer are caused by thermal effects induced by neighboring mountains. However, daily averages are not exceptionally high. Precipitation in 1985 was only 16.3 cm, as compared to mean annual precipitation of approximately 25 cm per year.

The pond data showed a standard deviation of 12 per cent in monthly water loss among ponds (Table 12.6). The Class A pan recorder and hook gauge showed an average deviation of 4.6 per cent based on monthly totals.

Actual evapotranspiration from the wetland cells was 0.8 of pan evaporation. This reflects differences in the energy budgets for the two situations.

Equations

Because of the limited data base, it was necessary to find a correlation, based on meteorological factors, to extrapolate to other years with different temperatures, insolation, humidity and wind. A large number of correlation equations exist in the literature, and are of two general types: those based on material and energy balances, and those based on purely empirical relationships.

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Table 12.5: Site comparison, summer (June, July, August)

	Houghton Lake, MI 1976	Carson City, NV 1985
T, °F	64	63
R, cal/cm ² day	405	596
Relative humidity, %	73	26
Wind, mph	82	99
Precipitation, cm	18.4	1.75
Pan evaporation, cm	25	69
Penman evaporation, cm	52	94

The Penman equation (Penman, 1948 and 1956) was selected as representative of the balance method, because it appeared to be a reasonable predictor of Heritage Ranch, Nevada pan evaporation when combined with the expected wind reach and crop type. That factor is 0.85 for which the Penman method yields the best estimate of the 1973-74 data for Heritage Ranch (Guitjens and Mahannah, 1975). Scheffe (1978) also chose the Penman Equation as the best available energy balance method for the Houghton Lake site.

Table 12.6: Water losses from wetlands treatment site, 1985 (cm)

Month	Heritage Ranch				Cells 1A-4D	Cell 8
	Pan 1973-1974	Pan (Recorder)	Pan (Hook Gauge)	Cells		
January	3.6	F	F			
February	8.7	F	F			
March	13.1	-	11.1			
April	16.8	19.2	16.6			
May	23.0	25.6	23.3			
June	23.2	31.1	33.5	25.6		24.4
July	25.0	32.9	31.8	25.9		
August	21.8	30.0	-			
September	16.8	15.8	-			
October	13.5	11.9	10.9			
November	8.9	-	8.6			
December	4.3	F	F			

Penman's formula is of the following form:

$$E = (SR_n + 0.27 E_a) / (S + 0.27) \quad (1)$$

where:

E = evapotranspiration rate in mm/day

S = slope of saturation vapor pressure curve at mean air temperature (T) in mm Hg/ $^{\circ}$ C

R_n = net radiation in cal/cm²-day

$$= R_t (1-\alpha) - R_b$$

R_t = total incoming solar radiation

α = albedo of surface

R_b = effective outgoing long wave radiation

$$= \sigma \cdot T^4 [0.180 + 0.250(10^{-0.126e})]$$

σ = Stefan Boltzman constant

T = air temperature, $^{\circ}$ K

E_a = a vapor flow parameter

$$= 0.35 (e_a - e_d)(0.5 + 0.01w)$$

e_a = saturation vapor pressure at mean air temperature in mm Hg

e_d = saturation vapor pressure at dew point in mm Hg
(thus $e_d/e_a \times 100$ = % relative humidity = R_H)

w = wind velocity at 2 meters above ground in miles per day

Typical results are shown on Figure 12.3 for the Houghton Lake site, with low values predicted compared to data. Carson City results are given in Table 12.7, and agree well with both cell data and modified pan data.

The Christiansen equation was chosen as the best empirical form available for the Carson City wetland, since it was developed for the same approximate latitude (Christiansen and Low, 1970):

$$E = K R' C_s C_t C_w C_h C_t C_c$$

where:

$$R' = \text{incoming radiation} \quad (2)$$

C_s = sunshine percentage coefficient

C_w , C_h , C_t = coefficients for wind, humidity and temperature,
with linear functions of W , R_H and T , respectively

HYDROLOGIC & WATER QUALITY VALUES OF WETLANDS

Table 12.7: Predicted water losses from wetlands treatment site,
1985 (cm)

Month	Cell data	0.8 x Pan	Penman	Grassi
January		-	4.1	1.1
February		-	8.1	3.8
March		-	13.3	6.4
April		15.3	17.6	17.0
May		20.5	24.0	22.0
June	25.6	24.9	24.2	23.6
July	25.9	26.3	24.4	24.7
August		24.0	20.6	22.4
September		12.3	12.4	10.8
October		9.5	8.7	6.8
November		-	0.0	3.0
December		-	0.6	1.8
7-Month totals (April-October)		132.8	131.9	127.3
12-Month totals			158.0	143.4

C_c = a monthly coefficient, which accounts for heat storage and crops/vegetation

K = a constant

In the present work, this has been slightly modified to make use of pyranograph data, which include cloud percentage, by using $R = R'C_s$. The resulting form may be written:

$$E = K R (b_t + a_t T) (b_w + a_w W) (b_n + a_n R_H) C_c \quad (3)$$

where:

R_H = relative humidity

Christiansen indicates that a similar form, with different coefficients, may be used for pan evaporation, E_p . Christiansen also suggests that an equation due to Grassi relates pan evaporation and marsh evapotranspiration reasonably well:

$$E = K' E_p C'_c \quad (4)$$

where:

C'_c = a new crop coefficient;

K' = a constant

Thus, $K'C'$ is the factor which converts pan evaporation into evapotranspiration in any given month. Monthly pan evaporation data were correlated with the Christiansen equation, with an average error of 9.5 per cent without using monthly coefficients. These cannot be determined from one year of monthly data. The resulting equation is:

$$E_p = K R C_t C_w C_h \quad (5)$$

where:

E_p = evaporation rate, inches/month

K = 0.51

C_t = 0.0451 $T - 1.157$

C_w = 1.45 - 0.0048W

C_h = 1.51 - 0.0049 R_H

R = incoming radiation, water inches/month

T = temperature, °F

W = wind, mph

R_H = relative humidity %

The average annual values of C_t , C_w and C_h , are all set to be 1.0, so 51 per cent of the average annual radiation results in evaporation. Christiansen found $K = 0.47$ for northern Utah. Other coefficients cannot be compared, because sunshine percentage was not correlated here.

Wind and relative humidity are of lesser importance than radiation and temperature. The monthly pan evaporation may therefore be correlated, with 13.5 per cent average error, with:

$$E_p = 0.50 R (0.0445 T - 1.130) \quad (6)$$

Daily coefficients can be determined from correlations of the daily values of water loss, although the errors associated with these readings are large, probably on the order of ± 20 per cent. These are caused by factors such as sticking recorder pens, wave motion, and chart reading uncertainty. Daily values were correlated with 25 per cent error.

The ratio of evapotranspiration to pan evaporation was determined for the June-July period, during which both sets of data were available. The monthly coefficient may be considered constant during this period, resulting in an average multiplier ($K'C'$) of 0.80. The data do not support further, monthly refinement of this multiplier.

The two predictors of evapotranspiration - Penman, and the Grassi modification of Christiansen - are shown in Table 12.7.

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Both agree, within a few per cent, on an evaporative loss of about 150 cm per year, based on 1985 climate.

Several factors bear on these predictions: first, it has been presumed that percolation does not exist in the cells tested. This is borne out by the close agreement of predictions and data; but also by the conservation of dissolved solids over the month of June. During that time, the water content of Cells 1B to 4D halved, and the electrical conductivity doubled, to within 10 per cent. Second, the dissolved solids concentrations, which range up to 15 parts per thousand, are not expected to affect evaporation (Harbeck, 1955).

Of course, none of these predictions works for the warm water wetlands, for which there was an average January evaporation of 2.2 cm/day.

The Thornthwaite (Thornthwaite and Mather, 1957) correlation was chosen as the best available empirical method for the Houghton Lake site. This involves a heat index I:

$$I = \sum_{1}^{12} (T/5)^{1.514} \quad (T = {}^{\circ}\text{C}) \quad (7)$$

Then a thermal term is computed from:

$$\text{UNPET} = \begin{cases} 0, & T < 0^{\circ}\text{C} \\ 10 [0.01 - 0.0245I]_T [0.467 + 0.017I] \\ 4.5, & T > f 26.5^{\circ}\text{C} \end{cases} \quad (8)$$

Radiation is computable from latitude:

$$R = a + b(\text{LAT}) + c(\text{LAT})^2 \quad (\text{LAT in degrees}) \quad (9)$$

Then, monthly potential evapotranspiration is the product

$$ET = R \times \text{UNPET} \quad (10)$$

This correlation produced low results, as shown in Figure 12.2, for the Houghton Lake wetland. It was very low for the Carson City wetland, probably because of the low cloud cover.

CONCLUSION

Water level records may be interpreted to give wetland evapotranspiration. However, great care must be used if the water table is below ground. The capillary suction may draw the well level down in preference to the soil, giving erroneously high readings. The potted plant work of Scheffe shown here, and perhaps that of others such as Bonde, Ives and Laurence (1961) were subject to this difficulty. When properly done, this method gives results which are supported by the water balance for the wetland (Hammer and Kadlec, 1986).

Pan evaporation is not a direct measure of wetland water loss, but is a good correlator of the meteorological driving forces. Pans are more consistent than Piche atmometers. Cover type and degree of shading have strong influences on pan evaporation, which shows high daily and seasonal variability.

Microcosm methods proved useful for both transpiration and for evapotranspiration. There are species differences in transpiration. The disadvantage of transpiration data taken in this way is that they must be accompanied by leaf weight standing crop data. The variabilities are compounded, preventing accurate estimates of a real water loss.

In any case, transpiration is not the sole water loss mechanism: it is accompanied by evaporation. When open water is present and leaves are not, evaporative losses predominate. Saturated soils may lose nearly as much as open water, but not if a litter layer is present.

The empirical correlations proved to be site-specific. The Christiansen equation, fit to Carson City conditions, seriously overpredicts Houghton Lake. The Thornthwaite equation, supposedly site independent, underpredicts both wetlands, but is worse for the western climate. The Penman method does an excellent job of predicting evapotranspiration for irrigated cropland near the Carson City site (Guitjens and Mahannah, 1975), but underpredicts wetland evapotranspiration. This energy balance method is the best of those tested. Discrepancies are attributable to the relationship between the wetland and the rest of the watershed. Neither site was large enough to preclude thermal and humidity influences from surrounding upland, as discussed by Morton (1983).

It is clear that more data are required before wetland evapotranspiration can be understood and quantified. For example, the presence of vegetation can create both positive and negative changes in water loss. Shading can cause water conservation, whereas transpiration can provide a parallel path and enhance loss of water as noted by Bernatowicz, Leszczynski and Tyczynska (1976). As wetland water management practice increases, definitive information must be available to achieve the desired goals.

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Chapter Thirteen

ROLE OF COASTAL MARSHES IN ENERGY DISSIPATION AND SHORE PROTECTION

Paul L. Knutson

INTRODUCTION

Many investigators have suggested that coastal marshes absorb wave energy and reduce erosion on estuarine shorelines (Gosselink, Odum and Pope, 1974; Rosen, 1980; Knutson, Brochu, Seelig and Inskeep, 1982). Others have concluded that with the use of agricultural techniques, marshes can often be established on shorelines where natural processes have failed to produce plant cover. Marshes established in this manner may greatly increase shore stability and reduce erosion (Phillips and Eastman, 1959; Sharp and Vaden, 1970; Woodhouse, Seneca and Broome, 1974, 1976; Dodd and Webb, 1975; Garbisch, Woller and McCallum, 1975; Knutson, Ford, Inskeep and Oyler, 1981; Webb, Allen and Shirley, 1984).

Though there is widespread agreement that coastal marshes provide shore protection, there is considerable doubt as to the magnitude and importance of this function. The following discussion will consider selected references on (1) wave energy dissipation and sediment capture, (2) sediment reinforcement, (3) shore protection, and (4) the management implications of these topics.

WAVE DISSIPATION AND SEDIMENT CAPTURE

Wave Damping

Dean (1978) suggested that marshes are much like an array of vertical cylinders in a water column. Based upon empirical estimates of the fluid drag forces occurring on vertical cylinders and laboratory observations of various arrays of cylinder, Dean developed a wave dissipation model for marshes. A series of field experiments were conducted to test the model in natural smooth cordgrass (*Spartina alterniflora*) marshes in Chesapeake Bay (Knutson et al., 1982). These experiments found the model with some modification to be useful for describing wave decay in these marshes. The model in modified form relates the ratio of incident wave height (H_1), seaward of a stand of marsh grass, and H_2 , landward of the stand of marsh grass as follows:

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$$\frac{H_2}{H_1} = \frac{1}{1+AH_1x} \quad (13.1)$$

where:

$$A = \frac{C_D C_P}{3\pi S^2 d}$$

and C_D = drag coefficient (approximately = 1.0), C_P = plant drag coefficient (approximately = 5 in smooth cordgrass), D = grass stem (culm) diameter, x = distance across marsh from seaward to landward through which waves propagate, S = average spacing of grass stems (assumed to be on square centers), and d = water depth. The plant drag coefficient (C_P) includes such factors as stem deflection and leaf characteristics. The plant drag coefficient can be empirically derived but will vary substantially between species and between marshes of the same species. Table 13.1 summarizes the average wave height loss and associated wave energy loss for the Chesapeake study as a function of the distance across the marsh the wave has traveled (x).

Table 13.1: Wave height and wave energy loss

Distance (<u>x</u>) (meters)	Wave height (H_1) (meters)	Wave height loss (%)	Wave energy loss (%)
2.5	0.15	40	64
5.0	0.15	57	72
10.0	0.17	65	88
20.0	0.16	87	98
30.0	0.18	94	100

Of importance here is that, on the average, more than 50 per cent of the energy associated with these waves dissipated within the first 2.5 meters of the marsh and that virtually no wave energy persisted at the 30 meter distance for the conditions evaluated.

As waves propagate through the marsh they experience an energy loss. The same process is involved when marshes are subject to current flow associated with tidally induced flooding. Under these conditions the plant stems dissipated the energy associated with unidirectional flow, diminishing the velocities of these currents.

Sediment Capture

As wave energy impacting a shoreline is reduced, there is increased potential for sediment deposition and decreased potential for erosion (sediment mobilization, suspension and transport). Sediment deposition resulting from marsh planting has been observed in both laboratory and field studies. Gleason, Elmer, Pien

and Fisher (1979) conducted a simple, yet informative laboratory experiment to determine whether retention of waterborne sand by smooth cordgrass was related to stem density. Waves generated in a laboratory apparatus were washed over a sloping beach planted with smooth cordgrass. They found that the amount of sand accumulated after 60 waves was a positive non-linear function of stem density. The greatest accretion coincided with the highest stem density tested. Accretion was more than 5 cm on a 3 per cent slope with a stem density of 108 stems/m² after only 60 waves. This phenomenon has also been documented in long-term field experiments. Woodhouse et al. (1974) reported vertical accretion of 15 to 30 cm of sediment along three planted shore profiles at Snow's Cut, North Carolina during a 2.5 year period.

Under conditions of abundant sediment supply, marshes can prograde seaward. A recent study of historic shoreline trends in Charleston, SC between 1939 and 1981 found net erosion on only 5 of 31 marsh stations (Michel, Kana, Hayes and Jensen, 1983). Some marshes were prograding at a rate of more than 10 m/yr. The accretionary environment of Charleston Harbor has been attributed to the 1942 diversion of the Santee River into a tributary which discharges into the harbor. Studies have shown that the diversion may be responsible for 85 per cent of harbor sedimentation (US Army Corps of Engineers, 1966).

Sedimentation processes are not confined to the margins of salt marshes. As energy is dissipated from tidal waters flowing across the marsh, they release their sediment burden. There is general agreement that coastal marshes are sinks for suspended sediments (Nixon, 1980). Estimates for annual accretion range from about 2 mm (Richard, 1978) to 18 mm (Redfield, 1972, Figure 31). Considering that energy dissipation is initially very rapid as water forces enter the marsh, it is to be expected that accretion rates are generally higher in areas adjacent to open water, stream banks or marsh margins. DeLaune, Patrick and Buresh (1978) measured accretion rates of 7.5 mm/yr in interior smooth cordgrass marshes and 13.5 mm/yr in streamside marshes in Louisiana. Similarly, in Connecticut accretion in the high marsh (saltmeadow cordgrass, *Spartina patens*) has been reported at 2-5 mm/yr (Harrison and Bloom, 1974, Nixon, 1980) while accretion in low marsh, smooth cordgrass, ranged from 8 to 10 mm/yr. Salt marsh accretion generally equals or exceeds local sea level rise (Nixon, 1980).

SEDIMENT REINFORCEMENT

Though it is empirically evident that the root systems of coastal plants improve soil stability, there is little experimental evidence on the subject. Gray (1974) summarized findings concerning soil reinforcement with vegetation in terrestrial soils. He noted that independent studies have shown that plant roots do significantly increase soil stability. In these studies roots or fibers increased shear strength by increasing apparent cohesion of the soil. The shear strength of vegetated soils was two to three times greater than that of unvegetated soils.

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A simplified approach to estimating the influence of plant root systems on soil shear strength considers only the average tensile strength of the roots (T_R) and the fraction of the soil cross-sectional area occupied by roots (A_R/A). The model assumes (1) a flexible, elastic root extending vertically across a planar shear zone and (2) that the tensile strength of the fibers is fully mobilized (i.e. they break in tension rather than pulling out) (Wu, 1976; Waldron, 1977; Brenner and James, 1977 in Gray and Leiser, 1982). Maximum shear strength increase from root or fiber reinforcement (ΔS_R - in units of mass/unit area) may be estimated to an average or first approximation by:

$$\Delta S_R = 1.15 T_R (A_R/A) \quad (13.2)$$

Few soil stability studies have been conducted on herbaceous plants (grasses or forbs). Waldron (1977) observed an increase in soil shear resistance of 1000 kg/m² (290 per cent increase) at a depth of 30 cm in soils vegetated with alfalfa (*Medicago sativa*). Unfortunately, Waldron did not report tensile strength (T_R) values or root area ratios (A_R/A) for the experiment (Gray and Leiser, 1982). Average tensile strength (T_R) values have been reported for woody vegetation ranging from about 100 to 600 kg/cm² (Gray and Leiser, 1982, Table 3.1). No data are available on the tensile strength of roots in coastal marshes. Though the author also knows of no direct measurements of root area (A_R/A) in marsh sediments, a conservative estimate of root area ratios can be extrapolated from annual root production estimates. Gallagher, Plumley and Wolf (1977) measured macro-organic matter (organic matter not passing a 1-mm sieve) in 18 coastal marshes on the Atlantic coast in order to estimate minimum annual below ground production. They reported annual organic production of from about 0.2 to 4.8 kg/m² (dry weight) in cores up to a depth of 0.55 m or a dry density of 0.4-8.7 kg/m³. Bulk dry density of marsh sediments (root matter and sediment) of 200 to 400 kg/m³ (McCaffrey, 1977; Delaune, Patrick and Brannon, 1976; Nixon, 1980), have been reported. If we further assume that the wet density of root material is approximately equal to wet sediment density (this is conservative and will tend to underestimate actual root volume) we can calculate a range of A_R/A values of 0.1 to 4.4 per cent. These root area ratios are relatively high when compared to woody species, particularly, if we consider the conservative approach used here in developing these ratios. Root reinforcement studies on tree species have reported root area ratios of 0.05-0.17 per cent (Wu, 1976) and 0.14-0.93 per cent (Megahan, Day and Bliss, 1978).

Field measurements of shear strength of tidal flat and tidal marsh (Pacific cordgrass - Spartina foliosa and pickleweed - Salicornia spp.) sediments were measured in two California Bays (Pestrong, 1969; Pestrong, 1972a; Frey and Basan, 1978) (Table 13.2). The increase in shear strength from channel and tidal flat to marsh, resulting largely from root reinforcement, is comparable to the 200 to 300 per cent increases reported by Gray (1974) for other vegetated soils. It is evident that field measurements of root ratios and the tensile strength of roots and additional measure-

Table 13.2: Shear strength in tidal sediments

Location	Shear strength (kg/m ²)
San Francisco Bay	
Channel	351
Tidal flat	522
Pacific cordgrass marsh	761
Pickleweed marsh	1,459
Tomales Bay	
Channel	410
Pickleweed marsh	1,279

ments of shear strength would greatly enhance our understanding of sediment reinforcement in marshes.

It is clear from the above that coastal marshes substantially reduce the susceptibility of shore sediments to erosion. The importance of shear strength is clearly illustrated when one examines the process of erosion in established coastal marshes. Marshes are not typically eroded by the mobilization of surface sediments because the marsh surface, as discussed earlier, is an energy dissipating environment. In established marshes erosion is frequently a more cataclysmic event, in which the marsh sediment fails (shears) in blocks on the margin of tidal guts (Redfield, 1972) or on the eroding seaward edge of the marsh (Pestrong, 1972b). The rate at which these blocks of marsh are carved from the marsh margin will be directly related to the shear strength of these marsh sediments.

SHORE PROTECTION

Erosion Control

Sea level is rising on a world-wide basis. An estimate of the global rise over the past 40 years of about 3.0 mm/yr has been made (Emery, 1980). This global rising of sea level (eustatic rise) is attributed to melting of polar ice (Flint, 1971; Emiliani, 1980) and thermal expansion of ocean waters due to increases in atmospheric temperatures (Gornitz, Lebedeff, and Hansen, 1982; Etkins and Epstein, 1982). However, the apparent rise in sea level is often greater (though more variable) if one considers changes in the elevation of coastal areas. Coastal subsidence is a common phenomenon in the United States due to ground water, gas and oil withdrawal. For example, because of the withdrawal of subsurface fluids (Leatherman, Kearney, and Clow, 1983) the Galveston Bay area is experiencing an apparent rise in sea level of about 4.0 mm/yr.

The influence of sea level rise on the shore can be visualized as the simple submergence of a slope, the slope being the coastal

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plain. However, geologists and coastal engineers usually prefer more complex models which emphasize beach profile adjustment resulting from rise in water level (Bruun, 1962; Dietz, 1963; Hands, 1981). In general, these models describe a landward (erosion) and upward displacement of the beach profile in response to sea rise. The concept of landward displacement of the shoreline is supported by reports that the majority of the world's beaches are eroding (Bird, 1980).

Chesapeake Bay, one of the world's largest estuaries, has one of the highest rates of tidewater erosion in the United States (Slaughter, 1964). Based upon limited data in Chesapeake Bay, Sabman and Batie (1979) suggested that coastal marshes exist primarily in areas with low erosion potential and that they erode at the same rate as fast lands exposed to similar winds, tides, currents and storms. However, Rosen (1980) conducted an extensive evaluation of the erosion susceptibility of the Virginia Chesapeake shoreline. He calculated shore erosion (period from 1860-1940) and classified shore environments along the Virginia portion of Chesapeake Bay. He classified bay shorelines as (1) impermeable beaches - sand veneer overlying impermeable, pre-Holocene sediments, (2) permeable beaches - sand, (3) marsh barrier beaches - sand veneer overlying marsh peat, and (4) marsh margins. Table 13.3 summarizes erosion rates associated with these four shoreline types.

Rosen also observed fringe marshes (marsh margin seaward of the beach) in association with all the above beach environments (approximately 10 per cent of the shore areas measured). When present, fringe marshes reduced the mean rate of erosion on impermeable beaches by 38 per cent, on permeable beaches by 20 per cent, and 50 per cent on marsh barrier beaches. Rosen concluded that the presence of salt marsh in the structure of the shore, either as a layer beneath the beach (marsh barrier), seaward of the beach (fringe marsh) or alone (marsh margin), results in the least-susceptible environment to shore erosion. Rosen also observed that the most extensive marsh development in the Virginia Chesapeake Bay correspond to the areas of highest local submergence (Holdahl and Morrison, 1974), areas where the greatest shoreline retreat due to sea rise would be expected.

Table 13.3: Erosion of shore environments, Chesapeake Bay

Shore type	Mean erosion (m/yr)
Impermeable beach	1.13
Permeable beach	0.85
Marsh barrier beach	0.66
Marsh margin	0.54

The increased stability of marsh shorelines was also observed in a recent evaluation of historic shoreline change in Galveston Bay. Leatherman et al. (1983, Table 4) measured mean erosion rates of 1.32 m/yr on sandy shores, 1.08 m/yr on silt-clay shores, and only 0.56 m/yr on marshy shores (rate calculated from the period 1850-1960).

A simple though critical concept is often overlooked in discussions of shore erosion. The 'shore' has been defined as 'the narrow strip of land in immediate contact with the sea, including the zone between high and low water lines ...' (US Army Corps of Engineers, 1984). The coast is 'a strip of land of indefinite width that extends from the shoreline inland to the first major change in terrain features ...'. 'Shore erosion' is then simply the loss of sediment from the intertidal profile while 'coastal erosion' is the wearing away of supratidal lands. Though the two terms are frequently used interchangeably (shore erosion being interpreted as a landward displacement of the 'shoreline', the intersection of the shore and the coast), considerable misunderstanding may arise when we are comparing the erosion of beaches and bluffs to the erosion of marshes. Erosion measurements from aerial photos (horizontal displacement of the shoreline) for beach and bluff environments are one dimensional measurements of shore and/or coastal erosion. However, similar measurements of erosion of the seaward margin of the marsh are not measurements of coastal erosion, because typically no wearing away of supratidal lands has occurred. Knutson et al. (1981) in an evaluation of 104 erosion control marsh plantings observed 'coastal erosion' in only 10 per cent of marshes that were 6 m or greater in width. The 'coastal erosion' rate of reaches of the shoreline fronted by broader marshes is negligible.

If we view the marsh as a coastal protection structure, the erosion rate of the marsh margin is not a measure of the performance of the marsh in abating coastal erosion. Rather, the marsh erosion rate (E_m) when considered in conjunction with marsh width (W_m) provides a useful estimate of the functional life (L_m) of the marsh as an erosion control structure:

$$\frac{L_m}{W_m} = \frac{W_m}{E_m} \quad (13.3)$$

The importance of this discrimination between shore and coastal erosion can be illustrated again using Chesapeake Bay as an example. Marsh acreage on the Virginia portion of the bay (excluding tributaries) is 1.3×10^8 m² (Wass and Wright, 1969). The length of marsh shoreline on these shores is 6.4×10^5 m. Average marsh width along this portion of the bay, considering the above, is about 200 m. If we further consider Rosen's (Table 13.3) erosion rate for these marshes of about 0.5 m per year, we would estimate that the average functional life of these marshes in slowing shore erosion and preventing coastal erosion will be about 400 years (equation 13.3).

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PRESERVING SHORE PROTECTION VALUES

Technical Issues

Two processes are critical to the preservation of coastal marshes during periods of sea rise - sedimentation and landward translation of the shoreline.

During periods of sea rise, marshes depend upon sedimentation (vertical accretion) to maintain elevations appropriate to sustain the growth of marsh vegetation. The lower Mississippi Delta is an extreme example of the results of sediment deprivation. The Delta has been deprived of sediment in part due to leveeing to provide flood protection and improve navigation and is subsiding due to natural processes and extraction of ground water, oil and gas. The result has been a massive submergence of the Delta's coastal wetlands. Losses due to submergence and accelerated erosion between 1956 and 1978 were estimated at 38,000 hectares (US Fish and Wildlife Service, 1980) and current estimates are nearly 10,000 hectares per year (Wicker, 1980). Though the submergence of the Mississippi Delta is not an isolated event, it is also not a common phenomenon in the coastal marshes of the US. As noted earlier, marsh features in coastal bays and estuaries commonly accrete sediments at a rate equal to or greater than the rate of sea rise (Nixon, 1980).

Traditionally, shore progradation has been viewed as the major process forming new marshes because of the major contribution that tributary deltas (Turner and Gosselink, 1975) and inlet flood tidal deltas (Godfrey and Godfrey, 1973) have made to the development of coastal marshes. However, the development of marshes on prograding shores is only one process that forms new marshes. The maintenance of marshes on eroding shores depend upon the landward migration of the marsh. A constructive feature of sea rise and subsidence is the submergence of the coastal plain and the landward translation of coastal marshes. The term 'marsh transgression' will be used here to describe this landward translation of coastal marshes due to sea rise and subsidence. The rate of marsh transgression (T_m) is a function of the flatness of the coastal plain (Δx = horizontal change; Δy = vertical change) and the rate of apparent sea level rise (S_r), the combined influence of eustatic (worldwide trends) sea level rise and isostatic (local trends) changes in land elevation:

$$T_m = (S_r) (\Delta x / \Delta y) \quad (13.4)$$

The contribution of this process in maintaining eroding marshes can be quite simply illustrated. If we assume a rate of sea level rise of 2 mm/yr (conservative by a factor of two for portions of the Gulf and Atlantic coastal plain) and an average slope of the coastal plain of 1 vertical to 500 horizontal (conservative at least for many areas of the mid-Atlantic and the gulf), we can calculate a potential marsh transgression of 1 m/yr. This potential transgression rate exceeds the 0.5 m erosion rate reported for the Chesapeake marshes (Table 13.3). If we consider that the change in width of an eroding marsh (W_m) for time interval (t) as:

$$\underline{W}_m = \underline{t} (\underline{T}_m - \underline{E}_m) \quad (13.5)$$

and \underline{T}_m = rate of horizontal transgression of the marsh due to sea level rise and \underline{E}_m = rate of horizontal erosion; we can see how an eroding marsh can maintain or even increase in width over time. The resultant width of an eroding marsh indicates that a disparity has existed for some period of time in which the rate of transgression has exceeded the rate of erosion. In the above example we could calculate an increase in marsh width of 50 m over a 100 year interval ($\underline{T}_m = 1$ m/yr; $\underline{E}_m = 0.5$ m/yr and $\underline{t} = 100$ yrs) despite an erosional loss of 50 m. The above is not intended to imply that due to sea level rise the overall abundance of coastal marshes is increasing. It is clear, however, that transgression is an important process in the maintenance of eroding marshes. Reference is made to the earlier observation by Rosen (1980) that the most extensive marsh developments in the Virginia Chesapeake Bay correspond to the areas of highest local submergence.

Management Issues

In the United States, the Federal and State statutes which ostensibly protect coastal wetlands, do so largely because of their biological values. The shore protection values of these wetlands continue to be relatively unnoticed. However, preservation for either biological or shore protection values are usually complementary objectives. Efforts to protect these values are likely to be successful only if we fully appreciate the processes that sustain coastal wetlands, sedimentation and transgression. Wetland protection is not simply the regulation of marsh fills or marsh excavations. Of the 38,000 hectares of coastal marsh lost from the Mississippi Delta (1956-1978), less than 15 per cent of the loss was due to direct modification (US Fish and Wildlife Service, 1980).

Many human activities can affect sedimentation in marshes including: flood control, fresh-water diversion, navigation improvements, and shore-protection measures. Public policy and practice commonly consider the impact of these activities on coastal sediment supply and, at least indirectly, seek to preserve the contribution of tributary and littoral sediments to coastal marshes. However, some human activities may be in direct conflict with sedimentation. Maintaining the waterways of the United States requires the annual dredging of approximately 300 million cubic meters of sediment (Blankmaship, 1975). Understandably, those responsible for maintaining navigation do not view coastal sedimentation as an asset. Earlier it was noted that Charleston Harbor marshes were for the most part prograding due to the diversion in 1942 of the Santee River into a tributary of the harbor. However, the diversion increased the annual maintenance dredging in Charleston Harbor from 400,000 m³ to 7,500,000 m³ (South Carolina Water Resources Commission, 1979). To reduce the massive dredging requirement, the Santee is being rediverted. One would expect that the rediversion will substantially change Charleston's coastal marshes. Frequently, the protection of navigation will be in direct conflict with preserving marsh sedimentation. Recognizing this potential conflict, the US Army Engineer Waterways Experiment

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Station (1978) initiated a nationwide study of salt marsh establishment on dredged material in the mid-1970s. It is clear from this work that there are many opportunities to devote a portion of the 300 million m³ of material dredged annually in the United States to the building of new marshes and the nourishment of existing marshes. There are also opportunities to redirect coastal tributaries to provide sediments to coastal wetlands. The most dramatic example of current diversion efforts are in the Mississippi Delta. Currently, the US Army Corps of Engineers has plans for a large scale, controlled freshwater diversion from the Mississippi into the coastal wetlands of southeast Louisiana (US Army Corps of Engineers, 1984; Chatry, 1985).

Earlier, the role of transgression in maintaining marshes on eroding shorelines was discussed. Though this process may be of substantial importance in maintaining marshes in coastal bays and estuaries, the concept is largely ignored in public policies and regulations concerning wetland preservation or coastal shore protection. Coastal dunes are analogous environments to marshes in several respects. Dunes function as flexible shore protection structures and they migrate landward in response to sea rise. In the late 1970s, a group of researchers proposed a comprehensive dune management plan for New Jersey based upon these attributes (Nordstrom, Psuty and Fisher, 1978; Gares, Nordstrom and Psuty, 1979). They used dune dimensions and shore erosion rates to define a 'Dune Management District' which consisted of both the dune and a zone of potential dune migration. The dune district was designed to provide protection from a design storm with a 50 year reoccurrence interval. The study then provided guidelines for practices that should be encouraged within the district which would maintain or enhance protective values. The principle of protecting not only the dune but also the potential area over which the dune must migrate to maintain its shore protection values is now in practice in many localities. A similar approach to the management of coastal wetlands would have merit. For example, a marsh management district might consider both the anticipated life of a proposed structure (t); local estimates of sea rise (S_r) and flatness of the landscape (Δx/Δy) to calculate an appropriate setback for a structure:

$$\text{Setback} = \underline{t} (\underline{S_r} x \underline{\Delta x / \Delta y}) \quad (13.6)$$

Considering a proposed structure with an anticipated life (t) of 50 years in an area experiencing sea rise of 2 mm/yr with a flatness (Δx/Δy) of 500/1, one could reasonably propose that the structure should be located at least 50 m from the marsh shoreline. Indeed, this is likely to be valuable information to the individual who is proposing the structure, whether or not the individual is interested in preserving coastal wetlands.

CONCLUSIONS

A comprehensive document on the functional values of wetlands was prepared by the US Federal Highway Administration - A Method

for Wetland Functional Assessment (Adamus and Stockwell, 1983). Quoting from that document, 'Wetland plants, like all plants, can bind soil with their root systems, but it is uncertain whether this process is effective enough to protect whole shorelines from erosion'. It should be clear to the reader at this point that marshes do in fact protect whole shorelines from coastal erosion. The above statement does, however, illustrate a common misunderstanding of the role of coastal marshes in shore protection. There is ample laboratory and field evidence to allow us to conclude that:

- (1) Coastal marshes dissipate energy associated with waves, currents, and storm surges.
- (2) The energy dissipation accomplished by marshes provides increased opportunities for sediment deposition and decreased potential for erosion.
- (3) The roots and rhizomes present in marsh sediments measurably increase sediment shear strength, reducing marsh erodibility.
- (4) Energy dissipation and root reinforcement in marshes produce measurable reductions in shore erosion and preclude coastal erosion.
- (5) An estimate of the functional life of a coastal marsh in providing shore protection can be made by dividing marsh width (landward to seaward) by the rate at which the marsh margin is retreating (landward).
- (6) The width of a coastal marsh, and therefore its functional life, can be increased through transgression (submergence of the coastal plain) provided vertical accretion of the marsh is equal to vertical rise in sea level.
- (7) During periods of sea level rise effective preservation of the shore protection values of coastal marshes requires attention to the processes of sedimentation and transgression.

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Chapter Fourteen

GROUND-WATER AND SURFACE-WATER INTERACTIONS IN MINNESOTA AND WISCONSIN WETLANDS

R.G. Brown, J.R. Stark and G.L. Patterson

INTRODUCTION

The interaction between ground water and surface water in wetlands is complex and depends on the hydrologic setting of the particular wetland. Hydrologic characteristics have been used in Wisconsin to classify wetlands into four categories; surface-water-depression wetlands, surface-water-slope wetlands, ground-water-depression wetlands, and ground-water-slope wetlands, as described by Novitzki (1978). The degree of ground- and surface-water interactions differs between the four categories.

Surface-water-depression wetlands are located in topographic depressions in low-permeability geologic materials. Inflow to these wetlands is from precipitation and overland runoff; outflow is by evapotranspiration and ground-water seepage. Ground-water seepage typically is small, as seepage is restricted by silt, clay, or bedrock underlying the wetland. Surface-water-slope wetlands occur along lakes and streams and readily exchange water with the adjacent surface water bodies. Ground-water-depression wetlands are similar to surface-water-depression wetlands, except that ground water depression wetlands receive significant ground-water inflow. Distinctive characteristics of ground-water-depression wetlands are that they are in good hydraulic connection with the regional water-table and there is no surface-water outlet. Ground-water-slope wetlands are located in the headwaters of drainage basins, receive water from the ground-water system, and surface-water outflow is significant. Ground-water and surface-water interactions vary with the type of wetland, from very little interaction in surface-water-depression wetlands to significant interaction in ground-water-slope wetlands.

The US Environmental Protection Agency began a study in April 1985, to quantify the hydrologic, chemical, and biological effects on wetlands of discharging secondarily treated wastewater from two small rural communities into wetlands as a tertiary-treatment method. As part of the overall study, the US Geological Survey was requested to determine the hydrologic and chemical effects of discharging the wastewater into the two wetlands. The purpose of this chapter is to describe and compare preliminary results of studies of the hydrology of the two wetlands, particu-

larly with respect to differences on ground-water and surface-water interactions.

METHODS AND MATERIALS

The wetlands selected for study are located near the wastewater-treatment plants for the communities of St Joseph, in central Minnesota (population 3,164), and of Phelps, in northeastern Wisconsin (population 612 winter, 1,050 summer). The St Joseph wetland is a ground-water-slope wetland on a topographically flat, glacial-outwash plain adjacent to the river that receives outflow from the wetland. The ground-water basin is approximately 1,400 acres. A ground-water divide exists between the wetland and river. The wetland covers 45 acres, of which 15 acres are primarily cattail (*Typha* spp.) marsh and 30 acres are tamarack [*Larix laricina* (Dee Roi) K. Koch] bog. Grassland and some isolated stands of hardwood forest surround the wetland. The surface-water drainage basin of the wetland covers 243 acres; 81 per cent of the basin is in urban land use. A storm sewer that empties into the wetland drains a large part of the basin. The ground-water basin discharging to the wetland is approximately 1,400 acres.

The Phelps wetland is a surface-water-depression wetland located in an area of steep topography (drumlins) underlain by sand and gravel deposits. The wetland, part of the headwaters for a small stream, covers 83 acres of mostly black spruce [*Picea mariana* (Mill.) B.S.P.], tamarack, and sphagnum (*Sphagnum* spp.) moss. The surface-water drainage basin of the wetland consists of 224 acres of hardwood forest.

Instrumentation and methodology used for data collection were similar at both wetlands. All components of the hydrologic budget were estimated from measurements taken in the field. Precipitation was measured with a network of four tipping-bucket raingauges with windshields and the two-axis method was utilized to estimate average precipitation over the basin as described by Bethlahmy (1976). Evapotranspiration (actual evapotranspiration was assumed to equal potential evapotranspiration because of constant saturation and open-water surfaces) was estimated from solar radiation, air temperature, and air humidity from a method described by Jensen and Haise (1963) and Jensen, Rob and Franzoy (1969). Surface-water discharge from the wastewater-treatment plant was measured with a laboratory-calibrated flume and water-level recorder. Natural surface-water inflows and outflows were measured with field-calibrated weirs and water-level recorders. Changes in storage within the wetlands were measured with topographic-map data and water-level recorders. Ground-water inflow and outflow were estimated from water-level data from a network of water-table wells and piezometer nests installed in and around the wetland, and from estimates of the hydraulic conductivity of the geologic units using lithologic information from well cuttings. A surface-water-flow model written by Leavesly, Lichtry, Troutman and Saindon (1983) was used to estimate the volume of overland flow to the wetland. The surface-water model simulates surface-water flow from both rainfall and snowfall (including snowmelt). A ground-water-flow

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model written by McDonald and Harbaugh (1983) was used to estimate flow volumes for the ground-water components of the hydrologic budget. The ground-water model simulates steady-state conditions (a simplification of long-term average conditions).

Errors associated with the calculation of each of the components of the hydrologic budget were estimated by methods described by Winter (1981). The errors were calculated as the standard error of measurement and are expressed as the percentage error in measurement of the component: (a) 9 per cent error in precipitation, (b) 18 per cent error in evapotranspiration, (c) 16 per cent error in surface-water inflow, (d) 12 per cent error in surface-water outflow, (e) 22 per cent error in ground-water inflow and outflow. These estimates of errors in measurement of each component represent only a qualitative comparison for the accuracy and not a quantification of error.

The data used in this paper were collected during May through December 1985 and, therefore, the hydrologic budget calculated is for that 8-month period only. The hydrologic budget was calculated using the following equation:

$$P + SWI + GWI = ET + SWO + GWO + S \quad (14.1)$$

in which P is precipitation, SWI is surface-water inflow (including overland flow and wastewater input), GWI is ground-water inflow, ET is evapotranspiration, SWO is surface-water outflow, GWO is ground-water outflow, and S is change in storage. The components of the hydrologic budget on the left side of Equation (14.1) are the inputs and the components on the right (except for S) are the outputs in the budget.

RESULTS AND DISCUSSION

The relative magnitudes of the hydrologic-budget components vary significantly between the two wetlands. The input and output components of the hydrologic budgets of the two wetlands were calculated as the percentage of the total input or output (change in storage was less than 5 per cent in both wetlands) and are listed in Table 14.1.

The volume of water that passed through each wetland during the 8-month study period differed significantly; 262 million gallons for St Joseph and 118 million gallons for Phelps. Precipitation as a percentage of the total input at the two wetlands was substantially different, with precipitation being the major percentage input to the Phelps wetland but only a minor percentage input to the St Joseph wetland. Surface-water input to the St Joseph wetland accounted for twice as much of the total input, on a percentage basis, as the surface-water input to the Phelps wetland. Ground-water inflow was a major percentage input to the St Joseph wetland but was insignificant at the Phelps wetland. The hydrologic budgets of the two wetlands differed significantly, which illustrates how inputs to the two wetlands contrast. The Phelps wetland is dominated by precipitation and the St Joseph wetland is dominated by ground water.

Table 14.1: Input and output components of the hydrologic budgets (% of total)

	St Joseph	Phelps
<u>Input components</u>		
Precipitation	16	77
Surface water	39	18
Ground water	45	<5
<u>Output components</u>		
Evapotranspiration	18	48
Surface water	82	47
Ground water	0	<5

Outputs from the two wetlands were predominantly evapotranspiration and surface water. Ground-water outflow from the St Joseph wetland was zero and was less than 5 per cent of the output from the Phelps wetland. Therefore, ground-water outflow is considered to be insignificant. Evapotranspiration and surface-water outflow are approximately equal at the Phelps wetland, whereas surface-water outflow predominates at the St Joseph wetland. The difference in the balance of evapotranspiration and surface-water outflow between the two wetlands probably is the result of the hydrologic settings of the wetlands. The Phelps wetland is located in a depression with surface-water outflow being restricted or ponded, whereas the St Joseph wetland is located in a sloped area and surface-water outflow is not as restricted. The ratio of precipitation to evapotranspiration is also important in describing the differences in hydrologic settings between the St Joseph and Phelps wetlands. The ratio of precipitation to evapotranspiration is 0.9 at the St Joseph wetland and 1.6 at the Phelps wetland. The larger ratio at the Phelps wetland indicates that precipitation greatly exceeds evapotranspiration and, in this particular wetland, results in surface-water outflow being an approximately equal part of the total outflow. In contrast, the smaller ratio at the St Joseph wetland indicates that precipitation and evapotranspiration are about equal and that the large percentage of surface-water outflow represents the export of surface- and ground-water inflows. The relative magnitude of each component in the hydrologic budget, as a percentage of the total input or output, illustrates the contrast in hydrologic settings of the two wetlands. The St Joseph wetland can be classified as a ground-water-slope wetland because there is substantial ground-water inflow and surface-water outflow. The Phelps wetland can be classified as a surface-water-depression wetland because ground-water seepage is small and surface-water outflow is restricted.

The large input of ground water to the St Joseph wetland also affects the chemical budget as ground water discharge upward through the peat underlying the wetland. This upward flow is evidenced by the potentiometric surface of the regional outwash aquifer, which is 2 to 3 feet higher than the elevation of the water

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level in the wetland. The low hydraulic conductivity of the peat restricts the rate of ground-water flow into the wetland from the aquifer. Ground-water input is insignificant at the Phelps wetland and the chemistry of precipitation (atmospheric deposition) greatly influences the chemical budget.

Approximately 80 feet of unsaturated material separates the Phelps wetland from the regional watertable. The unsaturated material consists of approximately 2 feet of peat, 6 feet of gray clay and silt, and 72 feet of sand and gravel. The clay and silt layer greatly restricts leakage of water from the wetland to the water table and, therefore, causes the wetland to be isolated from the ground-water system. Although there may be leakage through the clay layer, it is small compared to outflow from the wetland by evapotranspiration. The steep-sided drumlins surrounding the wetland have been found to contain thin, discontinuous sand lenses that allow limited ground-water flow into the wetland from the drumlins. However, this flow is small compared to the other inputs and probably makes up less than five per cent of the total.

Ground-water and surface-water interaction is evident at the St Joseph wetland and ground water significantly influences the hydrologic budget. The Phelps wetland is influenced primarily by precipitation, evapotranspiration, and surface water and there is virtually no interaction between ground water and surface water. The differences in hydrology of the two wetlands illustrate the importance of understanding the interactions between ground water and surface water before attempting to develop hydrologic budgets for wetlands.

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PART III
BIOLOGICAL VALUES OF WETLANDS

Chapter Fifteen

WETLANDS AND THEIR RELATIONSHIP TO MIGRATING AND WINTER POPULATIONS OF WATERFOWL

Frank C. Bellrose and Nannette M. Trudeau

INTRODUCTION

For at least six months of the year, waterfowl are away from their breeding grounds and located on migration and winter areas. Migration and winter areas, however, are considered a unit because they interact to provide the food resources necessary to sustain waterfowl until they return to their breeding grounds. When wetland resources along migration corridors are inadequate, waterfowl rely on food resources of winter areas for longer periods of time. As a result, waterfowl making the more direct and longer flights between breeding and winter areas are subject to increased survival constraints.

COMPOSITION AND FEEDING STRATEGY OF WATERFOWL

Dabbling ducks comprise 64.4 per cent of the waterfowl population that winters in the United States, bay diving ducks 12.8 per cent, sea ducks 1.2 per cent and geese 21.6 per cent. Dabblers search for food in the shallow waters of lakes, marshes, meadows, swamps, flooded fields and - in a few species - dry fields. Bay diving ducks usually find food in waters 5-40 feet deep in large interior lakes, and in coastal bays and estuaries. They feed extensively on molluscs, other animal life and aquatic plants. Sea ducks feed primarily on animal life found in the deeper parts of bays and sounds and in shallow, off-shore ocean waters at depths up to 100 feet. Geese, the most terrestrial of the waterfowl, derive a large part of their food from agricultural crops.

DISTRIBUTION OF WATERFOWL AMONG WETLANDS

The ecological grouping of waterfowl parallels their taxonomic grouping into tribes. These groupings provide rough parameters that can be used to distinguish the major wetland types used by waterfowl outside the breeding grounds. Because these wetlands are unevenly distributed across the United States, the distribution of the several waterfowl groups are similarly skewed. With the passage of time, waterfowl have established traditional breeding,

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migration, and winter areas to which their homing ability plays a key role. The routes and distances traveled from breeding to winter grounds depend upon the particular wetland attributes that provide the resting and food resources for survival.

Dabblers

Because dabbling ducks occupy shallow lakes, marshes, and swamps, they have a broader array of habitats available than divers. Surprisingly, the vast coastal wetlands of the Atlantic Flyway support only 4.6 per cent of the wintering dabblers in the United States (Table 15.1). Low use may be related to the distance of the Atlantic Flyway from the prairie breeding grounds or the lower production and reduced quality of carbohydrate foods available in the Atlantic Flyway.

Mallards (*Anas platyrhynchos*) and pintails (*Anas acuta*), the two most abundant dabblers and, indeed, the two most abundant of all ducks, are noted for their consumption of moist-soil weed seeds, mast, and grains, all high in carbohydrates (Bellrose, 1976). We believe that centuries ago, these dabblers exploited the mast-producing swamps and the seed-producing marshes and meadows associated with the grasslands of the interior and the Central Valley of California. Mallards outnumber pintails in the overflow bottomland hardwood area of the Mississippi Delta; however, pintails outnumber mallards on wetlands associated with former grassland biomes of the Great Plains and California (Bellrose, 1976).

Gadwalls (*Anas strepera*) and wigeons (*Anas americana*) are more prone to feed on the foliage of aquatic plants than on seeds (Bellrose, 1976). Where aquatic plants are abundant, these two species outnumber mallards and pintails, particularly in the coastal marshes of the Atlantic and Gulf of Mexico.

Bay Diving Ducks

The principal winter grounds of the bay diving ducks are the most distantly and laterally located in relation to the breeding grounds. Forty-eight per cent of the bay diving ducks migrate from western Canada to the Atlantic Coast, a decided eastward component to a north-south alignment. In flyways from east to west, the winter populations of bay divers are on a declining gradient, with the smallest numbers in the Pacific Flyway (Table 15.1). Among bay divers, only the redhead (*Aythya americana*) has a large component of its population (78 per cent) migrating on a north-south axis from prairie breeding grounds to the lower Texas coast (Weller, 1964). The canvasback (*Aythya valisineria*), sympatric to the redhead on the breeding grounds, migrates largely to Chesapeake and San Francisco bays, with only small numbers to the Texas coast. To reduce competition on the winter grounds and to improve chances for survival, these two species have evolved both geographically and ecologically different niches. Another species of this group, the ring-necked duck (*Aythya collaris*), reduces competition in winter by concentrating in swamps and marshes not used extensively by its congeners.

Table 15.1: The distribution of winter waterfowl populations in the United States by flyway, 1976-85

Flyway	Dabblers		Bay Divers		Sea Ducks		Geese		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%
Atlantic	684,000	4.6	1,421,000	47.7	196,000	67.4	1,036,000	20.6	3,337,000	14.3
Mississippi	5,131,000	34.1	725,000	24.3	3,000	1.0	1,554,000	30.8	7,413,000	31.8
Central	3,546,000	23.6	419,000	14.1	0	0.0	1,641,000	32.6	5,606,000	24.0
Pacific	5,665,000	37.7	413,000	13.9	92,000	31.6	804,000	16.0	6,974,000	29.9
Total	15,026,000	100.0	2,978,000	100.0	291,000	100.0	5,035,000	100.0	23,330,000	100.0

Source: Based on US Fish and Wildlife winter waterfowl inventories

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The greater scaup (*Aythya marila*) has evolved a more northern, more open marine wintering grounds which lessen its competition with the more abundant lesser scaup (*Aythya affinis*). Both species of scaup make extensive use of bays, sounds, and estuaries along the Atlantic and Pacific coasts. The lesser scaup occurs in greatest abundance on inland lakes and along the Gulf Coast of Louisiana (Bellrose, 1976).

Sea Ducks

Sea ducks, primarily eiders (*Somateria spp.*), scoters (*Melanitta spp.*) and oldsquaws (*Clangula hyemalis*), are limited during the winter months almost exclusively to the Atlantic and Pacific coasts in the United States (Table 15.1). Small numbers occur on the Great Lakes in the Mississippi Flyway, and accidental strays may occur farther west in the Central Flyway. Because their mollusc and crustacean food resources are so much greater in the coastal water of the Atlantic, wintering sea ducks are twice as abundant along the Atlantic coast than the Pacific (Table 15.1). Although often relying on the same molluscan foods as bay diving ducks, sea ducks reduce competition by feeding in deeper waters (Cottam, 1939).

Geese

With few exceptions, geese have the most directly north-south aligned migration corridors of all waterfowl (Bellrose, 1976). The Ross' goose (*Chen rossii*) has westward 'dog-legs' in its migration from breeding grounds adjacent to Queen Maud Gulf on the Arctic Ocean to the Merced National Wildlife Refuge in the San Joaquin Valley, California. The two marine geese, Atlantic brant (*Branta bernicla bernicla*) and black brant (*Branta bernicla nigricans*), migrate along the northern fringes of the continent and then to their respective coastal wintering grounds, the Atlantic brant largely to New Jersey and the black brant to Baja, California. Brant feed almost exclusively on marine eelgrass (*Zostera marina*), thereby utilizing an isolated food niche that enables them to avoid competition with other geese.

Other forms of geese have largely switched from natural goods to agricultural foods on migration and winter grounds. Races of Canada geese were the first to utilize waste grain in harvested corn, sorghum, soybean, barley, and wheat fields, and the green winter forage provided by clover and wheat (Bellrose, 1976). Only in recent decades have large numbers of snow geese (*Chen caerulescens*) turned from rootstocks, bullrush tubers, succulent shoots of cordgrass, and other marsh plants to waste grain in harvested fields of rice, barley, wheat, and corn. Because so much of their food is obtained from agricultural lands, the wetland requirements of geese are nominal and broad in scope. A water area protected from disturbance by humans and in proximity to an adequate food supply is the most important requisite.

The strong traditional homing by geese to specific migration and winter sites combined with their extensive use of agricultural

products as food has resulted in intensive management of strategic lands for geese by state and federal agencies. The north-south alignment of most of the Canada goose migration corridors across the continent relates to: (1) the ability of Canada geese to exploit agricultural crops for food, which has reduced their dependence on specialized wetlands that would require lateral displacement, and (2) the availability of adequate breeding areas in the Arctic and Subarctic, north of winter areas.

Differential Use of Wetlands as a Key to Survival

As the preceding discussion suggests, waterfowl of different tribes and species radiate from breeding areas to a wide variety of wetlands that provide the food they need to survive in the six or more months that they are away from the breeding grounds. By exploiting a variety of wetland niches, waterfowl are able to utilize food resources from wetlands that range from temporarily flooded fields to shoal coastal areas. By varying spatial and temporal activities, the 45 species of waterfowl native to North America have evolved traits that reduce competition among species to the minimum and exploit wetland resources to the maximum. Therefore, any change in the status of wetlands has a parallel effect upon the welfare of waterfowl.

STATUS OF WATERFOWL AND WETLANDS

Until 1955 no adequate data on the status of waterfowl in the United States existed, but waterfowlers generally agreed that duck populations declined greatly since 1900 (Phillips and Lincoln, 1930; Gabrielson, 1947). Prior to the Migratory Bird Treaty Act with Canada in 1918, excessive hunting and the loss of wetlands were considered to be the reasons for this dramatic decline (Day, 1959). Since 1930 the reduction in waterfowl abundance has been attributed largely to the loss or degradation of wetlands.

Declining Wetlands

About 215 million acres of wetlands occurred in the contiguous United States in the early days of settlement (Roe and Ayres, 1954). By the mid-1950s, 50 per cent of the original wetlands had been drained, leaving 108 million acres (Frayer, Monahan, Bowden and Graybill, 1983). Between the mid-1950s and the mid-1970s, wetland losses averaged 458,000 acres per year, largely as a result of drainage for agricultural purposes (Frayer *et al.*, 1983).

Declining Duck Populations

In recent decades, duck populations have continued to decline, especially mallard, pintail, black duck (*Anas rubripes*), canvasback, and redhead (Bellrose, 1976). Three important species have suffered appreciable reductions during 1970-85. Breeding numbers of mallards declined by 41.3 per cent, pintails 53.0 per cent, and blue-winged teal (*Anas discors*) 39.0 per cent (Bellrose, 1985). It

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is difficult to distinguish how much of this decline is due to lost wetland-upland nesting habitat on the breeding grounds or to wetland losses on migration-winter areas.

Mallards winter primarily in the overflow bottomland hardwoods of the Mississippi Delta, an alluvial plain that was formerly covered by 24 million acres of forest. At present, an estimated 4.5 million acres (less than 20 per cent) remain (Forsythe, 1985). Such a staggering loss of habitat has undoubtedly adversely affected the status of mallards, even though they have substituted waste grain (corn, rice, soybeans) as a partial replacement for lost natural foods.

About 56 per cent of the pintails wintering in the United States depend on the food resources of the wetlands and agricultural lands of California. Unfortunately, the loss of wetlands in California has been severe: 91 per cent of the original 5 million acres have been drained (US Fish and Wildlife Service, 1977). How much of the pintail decline is due to loss of breeding habitat and how much is due to the loss of winter food resources in California cannot be determined with certainty, but both factors appear to be important.

Most of the blue-winged teal winter south of the United States (Bellrose, 1976). The status of their food resources in Mexico, and Central and South America is unknown, and the recent decline of 39.0 per cent in breeding numbers may be related entirely to the loss and degradation of breeding ground habitats (Bellrose, 1985).

Public and Private Ownership of Wetlands

A survey of wetlands in the contiguous states by Shaw and Fredine (1956) provided data on wetlands available to waterfowl in the early 1950s. Of the 74.4 million acres of wetlands that were inventoried, 8.8 million acres were classed as of a high value for waterfowl, 13.6 million of moderate value, 24.1 million of low value, and 27.9 million of negligible value.

The proportion of high and moderately valued wetlands that are publicly owned is given by state for each of the four flyways in Table 15.2. Obviously, the decision to rate the value of wetlands by state criteria rather than on a flyway or nationwide basis has led to some misalignment of values; however, ratings by state permit us to make comparisons with public ownership and thereby to determine where the greatest needs for future wetland acquisition lie.

The best assurance that wetlands will be available for waterfowl is achieved when they are owned or controlled by public conservation agencies. Table 15.2 lists the acreage of state and federal refuges devoted primarily to migration and winter areas for waterfowl. Not all lands in waterfowl refuges are wetlands, and no reliable data on the proportion of wetlands in state and federal waterfowl management areas exist. A crude estimate is 50 per cent, with individual areas varying from 20 to 90 per cent in wetlands. In many cases, large acreages of upland are devoted to the production of agricultural crops, particularly where the management of geese is concerned. Over 10.6 million acres of wetland and upland habitats are currently found in state and federal waterfowl refuges

(Table 15.2). Depending upon the proportion of wetland acreage on waterfowl conservation lands, from one-quarter to one-half of the 22.4 million acres of wetlands classed as above average for waterfowl are publicly owned.

Shaw and Fredine (1956) reported the most extensive high quality wetlands for waterfowl were in the Mississippi Flyway. Although this flyway has the largest acreage among the four flyways in public ownership, that acreage amounts to only 32 per cent of the total (Table 15.2). In contrast, the acreage of waterfowl refuges in the Atlantic Flyway equals over 87 per cent of the more important wetlands. The Pacific Flyway has the fewest acres of wetlands rated high or moderate in value for waterfowl by Shaw and Fredine (1956). Because we did not consider wetlands of poor value for waterfowl and because waterfowl refuges contain uplands as well as wetlands, the data in Table 15.2 show a larger acreage of publicly owned waterfowl land in the Pacific Flyway than of existing wetlands. Only 28 per cent of the available waterfowl lands in the Central Flyway are publicly owned, the smallest proportion among the four flyways.

Waterfowl Density on Public and Private Wetlands

Table 15.3 compares the density of three tribes of waterfowl by flyway for wetlands rated by Shaw and Fredine (1956) as high and moderate in value for waterfowl. Density is also given for that of publicly owned waterfowl lands. Waterfowl numbers are based on winter inventory data for each flyway averaged over the years 1976-85. These data provide an index of use rather than an absolute comparison because winter inventories do not provide a complete coverage of all waterfowl populations.

On the basis of available wetlands, dabbling ducks increase in density across the United States from east to west (Table 15.3). Their density in lands under public ownership is lowest in the Atlantic Flyway and highest in the Pacific Flyway. If we isolate the density of dabblers in California, we find the highest use of public lands anywhere, 12.1 birds per acre per day. Bay divers had their greatest density both on the Atlantic Flyway wetlands as well as its public waterfowl lands. Geese use wetlands of the Pacific Flyway most intensely, but were most dense as prorated for the public lands of the Mississippi Flyway, followed closely by the Pacific (Table 15.3).

CONCLUSION

Waterfowl are dependent on wetlands for their life requirements, although geese and several species of ducks meet part of their fall to spring energy demands on the forage and grain provided by agricultural fields. As wetlands have been drained or degraded, duck populations have declined. The portion of that decline that can be ascribed to the loss of wetlands on migration and winter areas is unknown; however, on prairie breeding grounds the importance of wetland losses to the status of waterfowl is well documented.

Table 15.2: Comparison between public and private ownership of high and moderately valued wetlands important to migrating-wintering waterfowl

Flyway and State	Wetlands of high and moderate value ^a (acres)	State refuge (acres)	Federal refuge (acres)	Total public (acres)	Public ownership (%)
Atlantic Flyway					
Connecticut	14,900	7,500	300	7,800	52.3
Delaware	65,300	15,600	24,800	40,400	61.9
Florida	2,082,900	1,594,700	465,800	2,060,500	98.9
Georgia	461,300	41,000	467,900	508,900	100.0
Maine	160,700	19,300	30,300	49,600	30.9
Maryland	200,400	40,600	27,400	68,000	33.9
Massachusetts	102,300	14,000	10,900	24,900	24.3
New Hampshire	10,500	4,900	1,700	6,600	62.9
New Jersey	236,600	54,200	39,600	93,800	39.6
New York	135,500	57,000	23,200	80,200	59.2
North Carolina	119,600	11,100	232,700	243,800	100.0
Pennsylvania	23,700	41,100	8,900	50,000	100.0
Rhode Island	4,000	1,300	1,300	2,600	65.0
South Carolina	205,300	54,000	96,200	150,200	73.2
Vermont	16,200	10,200	5,800	16,000	98.8
Virginia	114,200	24,500	26,600	51,100	44.7
West Virginia	1,600	2,500	0	2,500	100.0
Flyway total	3,955,000	1,993,500	1,463,400	3,456,900	87.4
Mississippi Flyway					
Alabama	276,100	68,700	50,600	119,300	43.2
Arkansas	1,626,000	192,500	204,300	396,800	24.4
Illinois	271,800	126,900	89,900	216,800	79.8

Table 15.2 (continued)

Indiana	220,500	71,400	7,700	79,100	35.9
Iowa	108,700	136,600	66,800	203,400	100.0
Kentucky	111,800	27,100	2,000	29,100	26.0
Louisiana	2,413,000	562,100	328,000	890,100	36.9
Michigan	2,323,700	98,900	104,500	203,400	8.8
Minnesota	2,053,300	440,000	195,800	635,800	31.0
Mississippi	998,400	49,400	105,500	154,900	15.5
Missouri	198,800	59,300	43,200	102,500	51.6
Ohio	50,800	24,000	8,200	32,200	63.4
Tennessee	575,800	61,900	91,900	153,800	26.7
Wisconsin	437,700	363,400	154,300	517,700	100.0
Flyway total	11,666,400	2,282,200	1,452,700	3,734,900	32.0
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Central Flyway					
Colorado	68,700	30,600	0	30,600	44.5
Kansas	186,700	78,900	51,100	130,000	69.6
Montana	71,200	3,400	69,200	72,600	100.0
Nebraska	368,800	35,900	67,100	103,000	27.9
New Mexico	18,700	4,300	39,000	43,300	100.0
North Dakota ^b	1,208,500	44,800	287,300	332,100	27.5
Oklahoma	152,300	63,400	81,700	145,100	95.3
South Dakota ^b	575,600	120,800	42,700	163,500	28.4
Texas	2,184,200	28,200	287,000	315,200	14.4
Wyoming	7,700	3,300	19,400	22,700	100.0
Flyway total	4,842,400	413,600	944,500	1,358,100	28.0
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Pacific Flyway					
Arizona	27,900	4,700	63,700	68,400	100.0
California	494,000	55,100	288,700	343,800	69.6
Colorado	68,700	900	56,200	57,100	83.1
Idaho	82,400	35,900	79,100	115,000	100.0

Table 15.2: (continued)

Flyway and State	Wetlands of high and moderate value ^a (acres)	State refuge (acres)	Federal refuge (acres)	Total public (acres)	Public ownership (%)
Montana	71,200	40,900	53,700	94,600	100.0
Nevada	179,500	256,100	85,000	341,200	100.0
New Mexico	18,700	7,900	57,200	65,100	100.0
Oregon	322,800	46,500	286,300	332,800	100.0
Utah	591,500	76,900	94,500	171,400	29.0
Washington	108,200	254,500	162,800	417,300	100.0
Wyoming	7,700	32,500	14,800	47,300	100.0
Flyway total	1,972,600	811,900	1,242,100	2,054,000	100.0
Contiguous US total	22,436,400	5,501,200	5,102,700	10,603,900	47.3

Notes: a, Based on wetland acres of high and moderate value for waterfowl rated by Shaw and Fredine (1956)

b, Production areas omitted

Table 15.3: Number of migrating-wintering waterfowl per acre per day on wetlands of high and moderate value and on the proportion of those lands found in state and federal waterfowl refuges

Flyway	Dabblers		Bay Divers		Geese	
	Total acres	Public acres	Total acres	Public acres	Total acres	Public acres
Atlantic	0.17	0.20	0.36	0.41	0.26	0.30
Mississippi	0.44	1.37	0.06	0.19	0.13	0.42
Central	0.73	2.61	0.09	0.31	0.34	1.20
Pacific	2.87	2.76	0.21	0.20	0.41	0.39

Note: a, Based on wetland acres of high and moderate value for waterfowl rated by Shaw and Fredine (1956)

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The Mississippi Flyway contains the largest share of the 22.4 million acres of wetlands - 52.0 per cent, the Pacific contains the least - 8.8 per cent, the Atlantic Flyway has 17.6 per cent and the Central Flyway 21.6 per cent. The lowest proportion of wetlands in public ownership is found in the Central (28.0 per cent) and the highest in the Pacific (100.0 per cent), followed by the Atlantic (87.4 per cent). The Mississippi Flyway is only slightly higher than the Central Flyway in proportion of wetland in public ownership.

Based on waterfowl densities, future acquisitions of lands for waterfowl appear to be most needed in California, followed by the Central Flyway, and the bottomland hardwoods in the Mississippi Delta.

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Chapter Sixteen

AQUATIC HABITATS OF BREEDING WATERFOWL

George A. Swanson

INTRODUCTION

A unique combination of glaciation and climatic conditions in the Prairie Pothole Region has produced abundant, biologically productive wetlands (Leitch, 1964). Wetlands in a major portion of this region are dominated by a moisture deficit, and much of the surface water is non-integrated. Non-integrated basins have the potential to impound large volumes of water and undergo long-term, rather extreme changes in water depth and biotic conditions in response to climatic trends. An assessment of the role of wetlands in supporting breeding waterfowl must include the long-term cycles common to these dynamic aquatic ecosystems.

Several aspects of hydrology must be considered when evaluating the ecology of waterfowl and wetlands in the Prairie Pothole Region. Key factors are long-term hydrologic cycles and the role of the wetland complex in satisfying breeding requirements of waterfowl. The value of one wetland is a function of the presence of other wetlands that form a wetland complex.

Studies of wetlands and waterfowl feeding ecology were conducted in the Prairie Pothole Region of south-central North Dakota in order to assess relationships between breeding birds and aquatic habitats. The studies were designed to determine factors which influence foods consumed by breeding birds, food availability in wetlands and renesting characteristics. This chapter describes some of the results of these ongoing studies and reviews current literature on feeding ecology of breeding waterfowl in the Prairie Pothole Region.

METHODS

Feeding dabbling ducks were collected in the Drift Plain and Missouri Coteau physiographic regions of southcentral North Dakota during 1967-80 using methods described by Swanson and Bartonek (1970). Esophageal contents were measured via volumetric displacement and tabulated as described by Swanson, Krapu, Bartonek, Serie and Johnson (1974). Duckling distribution and chemical characteristics of prairie lakes were investigated in Stutsman and Kidder counties (Swanson, Adomaitis, Lee, Serie and

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Shoesmith, 1984). A wetland complex was selected in Stutsman County for a detailed study of the role of hydrology in influencing water chemistry and the combined influence of hydrology and chemistry on aquatic biota (LaBaugh, Winter, Adomaitis and Swanson, 1986). Plant community changes in response to water level and chemical changes were observed on the study area. Renesting characteristics of waterfowl were investigated on experimental ponds (Swanson, Shaffer, Wolf and Lee, 1986).

RESULTS AND DISCUSSION

Feeding Ecology

Invertebrates accounted for 97 and 99 per cent of the foods consumed by male and female northern shovelers (*Anas clypeata*), respectively, during the breeding season (Table 16.1). Crustaceans and small snails (gastropods) were the principal foods consumed. Cladocera (28 per cent), Anostraca (9 per cent) and Copepoda (9 per cent) were the dominant crustaceans consumed by paired females. Gastropods made up 36 and 32 per cent of the diet of males and females, respectively. Small pond snails (*Stagnicola* spp.) and planorbid snails were the most common molluscs consumed. Insects accounted for 9 per cent of the diet.

Gadwalls (*A. strepera*) feed on a diet dominated by plant parts during most of the non-breeding season. On the breeding grounds, however, invertebrates play a more important role. Breeding gadwalls selected a diet dominated by insects and by crustaceans larger than those consumed by northern shovelers (Table 16.1). Animal material accounted for 45 and 62 per cent of the diet of breeding gadwall males and females, respectively. Snails accounted for a small proportion of the diet even though they were abundant at the feeding sites selected. Midges (Chironomidae) and Cladocera were the dominant invertebrates consumed by gadwalls on seasonally flooded and slightly brackish semipermanent wetlands. Seeds accounted for only 10 per cent of the diet. Plant parts, particularly duckweed (*Lemna* spp.) and filamentous algae were important food items.

Studies of the feeding ecology of laying females in the Prairie Pothole Region of North Dakota have revealed high consumption of invertebrates. The invertebrate composition in the diet of laying dabbling ducks varied from 72 per cent for mallards (*Anas platyrhynchos*) and gadwalls to 99 per cent for blue-winged teal (*A. discors*) and northern shovelers (Swanson, 1985). Invertebrates also dominated the diet of female canvasbacks (*Aythya valisineria*), redheads (*A. americana*), lesser scaup (*A. affinis*) and ruddy ducks (*Oxyura jamaicensis*) collected in the Minnedosa area of Manitoba during the breeding season (Bartonek and Hickey, 1969; Siegfried, 1973).

Invertebrates dominated the diet of juvenile mallards in Manitoba (Perret, 1962) and immature blue-winged teal in North Dakota (Swanson, 1985) and were an important item in the diet of juvenile northern pintails (*Anas acuta*) collected in Alberta (Sugden, 1973). Plant parts, however, were dominant food items in the diet of juvenile gadwall and American wigeon (*A. americana*) in

Table 16.1: Aggregate volume (%) of foods consumed by northern shovelers and gadwalls collected during the breeding season in south-central North Dakota (1967-76)

Food item	Northern Shovelers		Gadwalls	
	Male n 28	Female n 44	Male n 36	Female n 72
Animal material	96.7	98.7	44.5	61.7
Gastropoda	35.6	31.9	0.0	2.2
Lymnaeidae	21.7	15.3	0.0	0.0
Planorbidae	12.6	14.9	0.0	0.0
Physidae	1.3	1.7	0.0	0.0
Miscellaneous Gastropoda	0.0	0.0	0.0	2.2
Crustacea	51.5	57.4	26.1	28.5
Ostracoda	0.4	2.7	4.8	4.8
Copepoda	12.5	8.9	0.0	0.0
Cladocera	17.0	27.7	16.4	14.7
Conchostraca	2.5	6.1	4.5	7.2
Anostraca	19.1	8.8	0.0	0.3
Miscellaneous Crustacea	Tr ^a	3.2	0.4	1.5
Insecta	9.0	9.0	18.4	30.5
Odonata	0.1	0.1	0.1	3.0
Heteroptera	Tr	0.3	0.6	0.4
Trichoptera	0.3	0.5	0.3	5.5
Coleoptera	Tr	1.6	0.4	3.2
Diptera	8.6	6.5	17.0	17.3
Miscellaneous insects	0.0	0.0	0.0	1.1
Miscellaneous animal material	0.6	0.4	0.0	0.5
Plant material	3.3	1.3	55.5	38.3
Seeds	3.3	1.3	9.9	9.6
Vegetation	0.0	0.0	45.6	28.7
Filamentous algae	0.0	0.0	15.1	9.6
<u>Potamogeton</u> spp.	0.0	0.0	9.1	2.3
<u>Lemna</u> spp.	0.0	0.0	16.7	9.1
Miscellaneous vegetation	0.0	0.0	4.7	7.7

Note: a, <0.1%

Alberta (Sugden, 1973). Juvenile canvasback and lesser scaup selected a diet dominated by invertebrates (Bartonek and Hickey, 1969) as did ruddy duck ducklings 1-5 weeks old (Siegfried, 1973). Juvenile redheads, similar to American wigeon and gadwall ducklings, selected a greater proportion of plant parts (Bartonek and Hickey, 1969). Sugden (1973) used dry weight to calculate proportions of plant and animal foods in the diet of ducklings he collected in Alberta.

Studies of foods consumed by Class I dabbling duck (*Anatini*) ducklings demonstrate high consumption of adult Diptera that are emerging or are in close contact with the water surface (Chura, 1961; Sugden, 1973). Class I blue-winged teal selected a diet

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dominated by small planorbid snails, amphipods (*Hyalella azteca*), and Heteroptera that were on the water surface or attached to aquatic plants in contact with the surface (Table 16.2). The diet of Class II and III blue-winged teal ducklings was less specialized. Midges increased in importance with age but the dominant forms consumed were larvae rather than adults. As the ducklings increased in size they were able to feed on benthic midges that became available on semipermanent wetlands during summer drawdown.

High consumption of invertebrates during the breeding season has been interpreted as a response to physiological demand for protein during egg production (Krapu and Swanson, 1975) and periods of rapid growth (Sugden, 1973). Invertebrates contain higher levels of protein than seeds or plant parts and also provide a better balance of essential amino acids (Sugden, 1973; Krapu and Swanson, 1975). Nesting dabbling ducks are often required to produce several clutches of eggs during the breeding season to compensate for high nest losses common to ground-nesting ducks in the Prairie Pothole Region (Cowardin, Gilmer and Shaiffer, 1985). Birds renesting in late June and early July have used most of their stored reserves during previous nesting attempts and must rely on the breeding grounds to supply nutrients required for renesting (Swanson, Meyer and Adomaitis, 1985). Wetlands that can supply abundant, highly available invertebrate foods must be available to satisfy these demands if waterfowl are persistently to renest in response to nest losses and successfully hatch a clutch.

Wetland Ecology

An important attribute of a prairie wetland complex is its ability to produce plants and invertebrates that can satisfy the different requirements of the breeding birds. It is not necessary for any individual wetland to meet all the requirements of breeding waterfowl if the sum of the capabilities of the individual wetlands, each with unique hydroperiods and water chemistry, provides the necessary resources. For example, mallards use several wetlands within their home range (Dwyer, Krapu and Janke, 1979) and with each renesting attempt may select a home range that encompasses different wetlands. As shallow wetlands dry, renesting birds feed in the central, open water zones of semipermanent wetlands. At this time emerging insects and invertebrates attached to submerged vascular plants that have reached the surface become available.

Small, shallow, seasonally flooded basins receive high use by breeding dabbling ducks when they contain water (Krapu, 1974; Kantrud and Stewart, 1977; Ruwaldt, Flake and Gates, 1979; Swanson *et al.*, 1985). These basins contain abundant populations of invertebrates that are available to breeding pairs and broods that feed in shallow water. The importance of small seasonally flooded wetlands is demonstrated during drought years when they are dry but the more permanent lakes and wetlands still contain water (Ruwaldt *et al.*, 1979). When shallow wetlands are dry breeding strategies are altered and production is reduced (Leitch, 1964; Ruwaldt *et al.*, 1979; Krapu, Klett and Jorde, 1983; Swanson *et al.*, 1985).

Table 16.2: Aggregate volume (%) of foods consumed by immature blue-winged teal collected during 1967-76 in south-central North Dakota

Food item	Class I ^a n = 24	Class II n = 20	Class III n = 24	Total n = 68
Animal material	100.0	91.5	95.3	95.7
Gastropoda	48.1	21.5	38.2	36.8
Lymnaeidae	0.5	8.4	7.7	5.4
Planorbidae	43.3	11.0	20.5	25.8
<u>Helisoma trivolvis</u>	1.5	5.0	7.9	4.8
<u>Gyraulus</u> spp.	41.8	5.9	11.1	20.4
<u>Planorbula</u> spp.	0.0	0.1	1.3	0.5
<u>Promenetus</u> spp.	0.0	0.0	0.2	0.1
Physidae	4.3	2.1	10.0	5.6
<u>Physa</u> spp.	4.3	0.0	5.1	3.3
<u>Aplexa hypnorum</u>	0.0	2.1	4.9	2.3
Crustacea	19.0	8.0	7.4	11.7
Amphipoda	19.0	2.7	0.1	7.5
Cladocera	0.0	5.3	7.3	4.2
<u>Daphnia pulex</u>	0.0	0.0	0.3	0.1
<u>Daphnia magna</u>	0.0	3.4	3.0	2.1
<u>Simocephalus</u> spp.	0.0	1.9	4.0	2.0
Hirudinea	0.0	0.2	1.9	0.8
Hydracarina	0.0	0.0	0.2	0.1
Insecta	32.9	61.8	47.6	46.3
Ephemeroptera	0.1	4.3	7.5	4.0
Odonata	5.8	5.0	6.6	5.8
Anisoptera	0.0	5.0	6.3	3.6
Zygoptera	5.8	0.0	0.3	2.2
Heteroptera	15.0	5.3	2.4	6.9
Corixidae	5.3	5.1	2.4	4.2
Notonectidae	0.0	0.2	0.0	0.1
Gerridae	3.0	0.0	Tr ^b	0.2
Mesovelidiidae	6.7	0.0	0.0	2.4
Trichoptera	0.4	0.0	Tr	0.2
Coleoptera	3.0	1.8	4.3	3.2
Diptera	6.0	34.7	26.8	22.6
Culicidae	0.0	0.1	0.0	Tr
Chironomidae	6.0	29.8	26.7	20.3
Larvae	2.6	22.3	21.1	14.9
Heleidae	0.0	2.3	0.1	0.7
Stratiomyidae	0.0	2.5	0.0	1.6
Miscellaneous insects	2.6	10.7	0.0	3.6
Plant material	0.0	8.5	4.7	4.3
Seeds	0.0	8.0	3.7	3.8
Plant parts	0.0	0.5	1.0	0.5

Notes: a, Gollop and Marshall (1954)

b, <0.1%

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The feather-edged basin morphology of prairie semi-permanent wetlands, when combined with the semi-arid climatic conditions that prevail, produces dynamic wetlands, e.g. small changes in water level produce major changes in the surface area exposed or inundated. Annually repeated seasonal alterations in water level maintain wet-meadow and shallow-marsh zones which, when flooded in spring, produce abundant invertebrate populations. Semipermanent basins cycle through occasional drawdowns that provide abundant invertebrate populations, annual seed crops, and perennial emergent plant cover in different phases of the cycle. When water levels decline during drawdown, benthic invertebrates such as midge larvae become available to dabbling ducks. Reflooding following drawdown established deep-marsh, shallow-marsh, and wet-meadow zones that can dominate the entire basin. High water conditions eliminate emergent vegetation producing basins with open water and wave-eroded shorelines. Waterfowl use is influenced by different phases of the cycle which alter plant and invertebrate communities.

As salt concentrations increase, species of plants and invertebrates change (Stewart and Kantrud, 1971; Swanson et al., 1984). Recently hatched ducklings cannot tolerate salt levels that exceed 20,000 $\mu\text{S}/\text{cm}$ and growth is retarded below this level unless spring seeps with fresh water are available (Swanson et al., 1984).

CONCLUSIONS

Prairie wetland complexes contain a variety of wetlands that vary in hydroperiod and salinity and, subsequently, produce plant and invertebrate communities that support different stages in the reproductive cycle of waterfowl. Plant and invertebrate communities are hydrologically manipulated by: (1) annual fluctuations in water level that establish and maintain different wetland zones, (2) long-term trends in climatic conditions that cycle semipermanent lakes between extremes of flooding and drawdown, and (3) surface and ground water flow systems that interact with basin topographic setting to control salt concentrations. These hydrologic events manipulate the biotic communities of a wetland complex and subsequently support breeding waterfowl throughout the breeding season. Our ability to manage plant and invertebrate communities that support breeding waterfowl will depend on our knowledge of the hydrologic factors that control their distribution.

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Chapter Seventeen

COASTAL WETLANDS - MAJOR ECOLOGICAL ENTITIES FOR WADING AND SHORE BIRDS

S.A. Hussain

INTRODUCTION

Just under 100 species of shore and wading birds belonging to ten families occur in the Indian subcontinent and adjacent oceanic islands, of which roughly 46 per cent are resident and the rest migrant (Table 17.1). The breeding populations of north and central Asia wading birds move southwards into the Indian subcontinent, and commence their fall migration by mid-August, reaching a peak in late October.

Charadriidae comprise the largest numbers. Although most of these species prefer estuarine areas, nearly all of them also feed in freshwater conditions, since the migration from breeding areas covers vast tracts of landmass. A discussion of each family follows.

- (1) Ardeiidae: Of the 20 species found, only two, Ardea goliath and Botaurus stellaris, are rare winter visitors. These species are predominantly fisheaters, and both resident and local migrants occur in freshwater as well as estuaries. Local movements are mainly determined by water conditions and food availability.
- (2) Ciconiidae: These species are the largest of the waders adapted to a variable animal diet, but mostly eat fish. Two species, Ciconia ciconia and C. nigra, are winter migrants from central Asia. Two of the most common, Mycteria leucocephala and Anastomus oscitans, are colonial nesters in mixed species heronries. Both feed in freshwater as well as estuarine areas.
- (3) Threskiornithidae: These four species are nomadic, moving for considerable distances depending on water conditions. They are colonial nesters and prefer to nest in mixed heronries.
- (4) Phoenicopteridae: Both Phoenicopterus ruber and Phoeniconaias minor breed in the Rann of Kutch and disperse in the peninsula and Sri Lanka. A migratory population,

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Table 17.1: Shore birds and waders of the Indian subcontinent

Family	Species numbers		
	Total	Resident	Migrant
Ardeidae	20	18	2
Ciconiidae	8	6	2
Threskiornithidae	4	4	-
Phoenicopteridae	2	2	-
Haematopodidae	1	-	1
Rostratulidae	1	1	-
Recurvirostridae	2	1	1
Dromadidae	1	-	1
Burhinidae	2	2	-
Charadriidae	58	12	46
Total	99	46	53

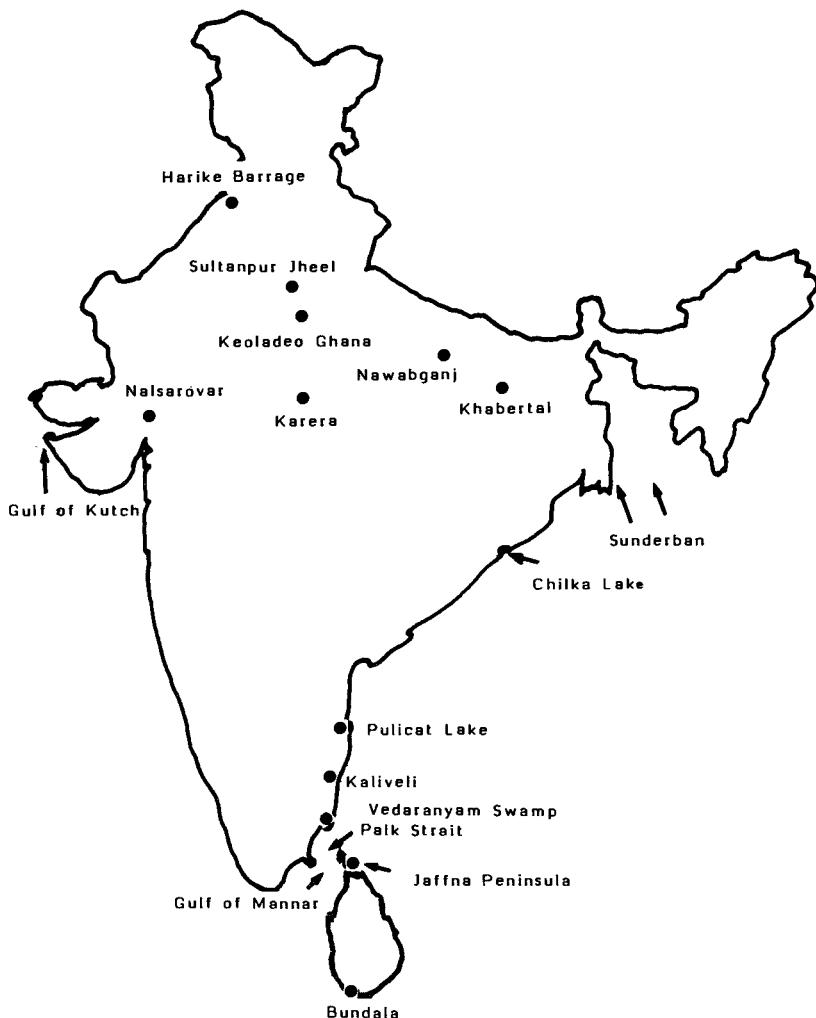
possibly from western Asia winters together with the local populations.

- (5) Haematopodidae: This family has only one holarctic species wintering along the coast. Small flocks move along rocky coastlines.
- (6) Rostratulidae, Recurvirostidae, Dromadidae and Burhinidae: These four families comprise six species altogether, of which Recurvirostra avosetta and Dromas ardeola are mainly winter visitors. One species, Burhinus oedicnemus, occurs inland in dry rocky country.
- (7) Charadriidae: This is the largest family, comprising 46 migrant and 12 resident species. Calidris minutus and C. testaceus form the bulk of the population, followed by Charadrius mongolus, Philomachus pugnax, Tringa glareola (both partial to freshwater) and T. totanus.

Wetlands of Kashmir Valley and the Indo Gangetic Plains provide a broad spectrum of dispersal ground for some of the shore and wading birds adapted to feed in freshwater conditions. Most migrants spread out along the eastern and western coasts of the peninsula, including the islands of Sri Lanka, Andaman and Nicobar group (Figure 17.1).

India has a vast coastline stretching over 3,600 km with sandy shores, mangrove backwaters, lagoons, mudflats, estuaries

Figure 17.1: Location of the major wetlands in the Indian peninsula



and large brackish/saline lakes adjoining the coast (Table 17.2). The peninsular land mass is flanked by the Arabian sea in the west and the Bay of Bengal in the east. The major coastal wetlands which attract larger number of wading and shore birds are the Gulf of Kutch, Vedaranyam estuary in the southeast, Pulicat Lake, and the Chilka Lake. In the southern tip, the Gulf of Mannar and adjacent coast on the peninsula, as well as the island of Sri Lanka, have a constant shift of shore bird populations.

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While most of the shore birds range over the coast and several thousand water bodies throughout the country, there are at least two major estuarine wetlands which host large concentrations of shore birds. These are Chilka Lake in the State of Orissa and Great Vedaranyam Estuary in Tamil Nadu.

The data below are based on field studies carried out by the Bombay Natural History Society at two major coastal wetlands: the Vedaranyam Swamp ($10^{\circ}18'N$; $79^{\circ}51'E$) in Thanjavur district, Tamil Nadu; and Chilka Lake ($19^{\circ}28'N$; $85^{\circ}6'E$) in Orissa State. Funds for the project were provided by the US Fish and Wildlife Service, routed through PL-480 rupee funds in India. The Indian Department of Environment and Wildlife Departments of Tamil Nadu and Orissa provided facilities for research work in the field. Ecological profiles of Vedaranyam and Chilka are presented here in two sections.

VEDARANYAM SWAMP

Environment

The Vedaranyam Swamp stretches 20 km westward from the promontory of Point Calimere ($19^{\circ}18'N$; $79^{\circ}51'E$). The western boundary is composed of mangrove vegetation, while the rest of the area is mostly open mudflat and lagoons. The 24,000 hectare swamp is interspersed with numerous small islets. The entire swamp is screened off from the Palk Strait, which forms the southern boundary, by a long spit or sandbar breached at various places by inlets and outlets for water flow. Five freshwater channels empty into the swamp which maintain the freshwater content of the large lagoon in the center of the swamp. The swamp is flanked on the north by an artificial berm beyond which villages and cultivated areas occur.

Profiles

Climate. Situated at the spur of the promontory, the area bears the brunt of periodic cyclonic storms that lash the Coromandal Coast. The rainy season commences around October with the onset of the North-East monsoon. The average annual rainfall between 1960 and 1979 was approximately 127.3 cm with the greatest precipitation recorded in the months of October, November and December.

Vegetation. The vegetation of the estuary comprises:

- (1) Tropical dry evergreen forest (Point Calimere);
- (2) Mangrove forest (estuary, lagoon, etc); and
- (3) Seashore vegetation.

Temperature, salinity and prolonged dry periods show extensive variations in the phenophases of the vegetation of the area. Data collected for three years (1980-83), showed that the flowering and fruiting season varies among species, sometimes even in the same species.

Table 17.2: Major wetland areas in the Indian peninsula

Sea board	Freshwater
Gulf of Kutch - Gujarat	Harike Barrage - Punjab
Gulf of Mannar - Tamil Nadu	Keoladeo Ghana - Bharatpur, Rajasthan
Palk Strait - Tamil Nadu	Karera - Madhya Pradesh
Vedaranyam Swamp - Tamil Nadu	Nalsarovar - Gujarat
Pulicat Lake - Tamil Nadu/ Andhra Pradesh	Khabertal - Bihar
Kaliveli - Pondicherry/ Tamil Nadu	
Chilka Lake - Orissa	Sultanpur Jheel - U.P.
Jaffna Peninsula - Sri Lanka	Nawabganj - U.P.
Bundala - Sri Lanka	
Sunderbans - West Bengal/ Bangladesh	

Invertebrates. More than 575 species of insects belonging to 16 orders were recorded from the Point Calimere area. Population counts of these were also made on a regular basis with standard methods. An initial perusal of the population dynamics shows the increase in the bird population coincides with an increase in insect population.

Estuarine benthos. The great Vedaranyam Swamp, according to the classification of Cowardin et al. (1979) is an estuarine and subtidal system with unconsolidated bottom. It is a conglomerate of mangrove swamps with coastal salt flats without submerged vegetation and coastal, open brackish water with patches of aquatic bed and an irregularly flooded forested wetland. The water chemistry ranged from hyperhaline to euhaline and mixohaline fresh. The entire area is transformed into a nearly freshwater lagoon during the peak of the rainy season. In the lean period, especially in summer, salinity increases as most of the mudflats dry up and get periodically flooded due to high tides or excessive wind action. The estuary is very rich in micro- and macro-organisms, and these are spread out in numerous micro-habitats.

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Seashore. The actual seashore is confined to the easternmost portion of the swamp. Here, fine sand, perpetually washed by wave action, harbors a variety of shore crabs, molluscs, coelenterates, amphipods, holothurians, isopods, littoral polychaetes and several other intertidal epifauna. The fine, sandy seashore gives way to a more silty-loamy shoreline westwards where, due to the sheltered nature of Palk Strait, the shoreline decreases considerably. Beyond this mangrove swamps predominate, and mudskippers (*Periophthalmus* sp.) and other burrowing organisms are abundant.

Mudflats. Mudflats which occur on the leeward side of the seashore are subject to variations in water levels caused by periodic flooding during high tide, excessive wind action, and by overflow from freshwater inlets. The soil is mostly clay and silt, and the fauna is predominantly of burrowing types.

This zone is rich in molluscs, blind gobids, and certain species of eels and crabs. At the onset of the monsoon, shrimp breeding takes place in the area, and these, along with other breeding fish, provide abundant food for piscivorous birds.

Lagoon Environs. Landwards, the character of the micro-habitat changes slightly from the mudflats where freshwater channels bring in fresh silt deposits resulting in a rich clay-silt-ooze formation. Shrimps, amphipods, molluscs (Donax, Solen, Katelysia and Mya), crabs Scylla, Neptunea, and fish (Stolephorus, Tachysurus, Mugiltiza, Therpon and Hemiramphus) occur in this area. The varied range of water depths (shallow to deep water) provides ideal niches for a variety of bird species to feed. In fact, this zone receives large concentrations of wintering as well as resident waterfowl.

Man-made Environments. Alterations in ground conditions made by man for manufacture of salt near Vedaranyam in the easternmost portion of the estuary has given rise to different types of zonation both for epifauna and predator species. The three-year studies at Point Calimere show that these artificial reservoirs produce a steady source of food for wading and shorebirds by virtue of the constant flooding and creation of habitats. However, at present these artificially created environments are used purely on commercial considerations, and as such, whatever benefit that is derived by birds from such a system is purely coincidental.

Avifauna

Species composition. The Point Calimere sanctuary and the adjacent estuary hosts six distinct groups of avifauna: (a) resident, (b) transient, (c) local migrants, (d) wintering migrants, (e) breeding migrants and (f) over-summering populations. Over 230 species of birds have been recorded so far from the area. Of these, almost 14 per cent are permanent residents, 32 per cent are local migrants, including five species, Podiceps ruficollis, Esacus

magnirostris, Charadrius dubius, C. alexandrinus and Sterna albifrons, which are also breeding visitors. Long-distance migrants from as far as arctic Russia comprise 33 per cent of the population. Other species are mostly transients, occasional visitors and stragglers.

Though fruiting occurs throughout the year, very few frugivores exploit it fully. Fish-eating waders occur throughout the year. Their peak population occurs during February/March when food is abundant.

Of the species recorded to date, 38 per cent feed on littoral/aquatic elements. Birds of prey constitute 8 per cent and granivorous/frugivorous species constitute less than 8 per cent. Insectivorous species of which the majority are migrants, comprise 27 per cent and the rest are omnivorous.

Ecological Consideration

Point Calimere Sanctuary and the adjacent salt swamps are the major important estuarine components in the east coast of India. The richness and diversity of the biomass available here attracts a vast number of migratory waterfowl in winter. A recent increase in fishing activity in the area also underscores its potential as a major biological entity. However, this area has been generally overlooked so far by research biologists and others. The neglect is further emphasized by the fact that only a few published papers are available on the estuarine fauna or flora of the area.

Conservation Outlook

It is likely that economic consideration and human population pressures will eventually lead to (a) over-exploitation and consequently depletion of resources, and (b) habitat alteration which will have a detrimental effect on the regenerative cycle of resources as well as destruction of the habitat. In the long run, this great wetland may lose its potential as a dynamic system and as a major source of both wintering grounds for birds and livelihood for humans. In the meantime, unless we act now, one of the largest and most productive estuarine systems in India will degenerate without being studied, understood and preserved.

CHILKA LAKE

Environment

Physiography. Chilka lake, with an area of 1040 km² is the largest brackish water lake in India. It is connected with the Bay of Bengal through a channel 29 km long and 365 m wide. The lake is between latitudes 19°28' and 19°54'N and longitudes 85°6' and 85°35'E.

Nalban Island. The island is located almost mid-way between north-south in the lake, and is about 12 km from the main fishing village, Balugaon. Nalban, a weed-covered marsh in Oriya, is a

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shallow marsh of about 10 km² which is completely inundated during the monsoon months. The water level gradually recedes to about 2-3 ft around October-November when aquatic vegetation emerges. During this period the local fishermen build a network of dykes and canals to maintain a low, inundated area where large-scale fishing operations take place until about the middle of February. Between December and February a large number of fish-eating ducks and smaller waders, flock in this area either to feed or to roost. The island completely dries up by March and large numbers of cattle from the surrounding villages graze on the vegetation.

Profile

Climate. The area receives rainfall during the months of August to October. Temperature, water depth and salinity (Table 17.3) vary according to the seasons, tidal action, and periodic drainage from feeder rivers.

Epi. and Infauna. The bottom fauna of Chilka forms a very important source of food for some groups of fishes, and their distribution and abundance have received increased attention in recent years (Table 17.4).

Vegetation. In most of the lake, the aquatic vegetation is scanty. The predominant aquatic species that occur in Chilka are: (1) Potamogeton spp.; (2) Halophila ovata - a species that creeps along the bottom, sending up stems of four to six inches high at short intervals; (3) Phragmites sp. - a semi-aquatic flowering plant which is by far the most conspicuous reed that covers Nalban Island.

Avifauna Profile

The lake hosts over 150 species of birds in the peak winter migratory season. Of these 32 per cent are aquatic, 22 per cent waders, and about 46 per cent are terrestrial birds. The last includes 14 species of birds of prey. Major concentration occurs from about early October to mid-March, when most of the winter waterfowl arrive and spread out along the lake.

Due to the vastness of the lake it is extremely difficult to determine the number of birds that are either on passage or are wintering in the area. Constant shifting of feeding grounds along the lake makes it extremely difficult to gauge the species composition and relative abundance of the individual species. Large flocks of birds scatter throughout the lake. The major concentration in terms of species abundance are dabbling ducks (Anas penelope, A. strepera, A. clypeata and A. querquedula). Diving ducks (Aythya nyroca, A. ferina and A. fuligula) spread out throughout the lake, may actually be greater in number than other species of ducks. The other diving species, Fulica atra, also occurs in deeper parts of the lake.

Table 17.3: Physicochemical features of Chilka Lake

Factors	Max.	Month	Min.	Month
Water temperature	32°C	June 1958	19°C	Jan. 1960
Air temperature	31°C	June 1959	17°C	Dec. 1959
Salinity (%)	36.2	May 1954	0.16	Oct. 1958
Dissolved O ₂	11.4 ppm		3.3 ppm	
pH	9.6		8.0	
Alkalinity	122 ppm		26.6 ppm	

Birds of Prey. Fourteen species of birds of prey have been recorded. Of these, six species were observed over Nalban Island. Large concentrations of prey species in this area appear to attract them to the island.

Waders. Both long- and short-legged waders congregate in large numbers on the island. Phoenicopterus roseus, Phoeniconaias minor, Ardea cinerea, A. purpurea, Egretta garzetta, E. intermedia, Platalea leucorodia, Mycteria leucocephala and Threskiornis aethiopica constitute the majority of long-legged waders. Ardeola grayii Nycticorax nycticorax, are abundant as the water dries up. Long-distance migrants constitute the majority of short-legged waders. Of these, the most noteworthy records have been Eurynorhynchus pygmaeus and Limnodromus semipalmatus.

Gulls and Terns. Larus brunnicephalus and L. ridibundus constitute the majority of gulls. Seven species of terns were recorded, of which, one, Sterna albifrons, breeds on the island.

Breeding birds. When Nalban Island dries up in the latter half of March, it provides excellent nesting sites for five species of bird, Sterna albifrons, Gelochelidon nilotica, Himantopus himantopus, Alauda gulgula and Glareola pratincola.

Ecological Considerations and Conservation Outlook

The rich ecological diversity and the sheer vastness of the lake makes Chilka one of the most important coastal wetlands on the Indian peninsula. Substantial baseline data such as the fauna, flora, and physiography are available. In recent years, a great deal of commercial exploitation of the lake resources has taken place both by government agencies and by the private sector. The State Government has plans to develop the area as a tourist attraction. Human populations near the islands and in peripheral

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Table 17.4: Species of the bottom fauna of Chilka Lake

Group	No. of species
Sponges	7
Polychaeta	33
Oligochaeta	1
Hirudinea	6
Copepoda	58
Cumacea	2
Decapoda	54
Gastropoda	34
Lamellibranchiata	45
Polyzoa	3
Isopoda	15
Coelenterata	20
Echiurdoidia	2
Ctenophora	11
Stomatopoda	3
Nudibranchiata	2
Fish	118
Amphipoda	17

villages and towns has increased considerably. There is, in effect, year-round pressure on the lake resources which needs to be assessed and precautionary measures taken. A beginning has been made by the declaration of the entire lake as a sanctuary for waterfowl under the Ramsar Convention of Wetlands. However, a careful assessment will have to be made to develop a useful management plan for the area.

Another disturbance in Nalban is the presence of a large number of domesticated buffaloes. The abundance of fresh grass in the island, which is separated by only 2-3 km of shallow water from the revenue villages on the eastern shore, makes it an ideal place for the villagers to leave their buffaloes for grazing. During February and March, there were about 400 buffaloes on the island, of which 95 per cent were emaciated bulls.

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Chapter Eighteen

MAMMALS AND WETLANDS¹

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INTRODUCTION

Of the approximately 4,200 species of mammals inhabiting the earth, few are singularly adapted for existence in wetland environments. Yet wetland habitats provide important resources for many mammals that occupy broad ecological niches but are typically associated with other habitat types. With an overall goal of seeking common trends, the specific purposes of this chapter are: (1) to review the importance of wetlands as habitats for mammals and (2) to discuss the contribution of mammals to wetland ecosystem dynamics.

As used herein, wetland mammals are terrestrial or semi-aquatic mammalian species that commonly use wetlands for cover or obtain a major portion of their diet from wetland-dependent organisms. This definition is arbitrary, and for purposes of this chapter, it does not include any of the volant bats (Chiroptera) or aquatic manatees (Sirenia). Although I am not aware of any bats which are limited to wetland habitats, wetlands no doubt contribute to the welfare of many species by providing trees for roosting or foraging sites, or enhancing prey availability. Also, manatees may be important herbivores in tropical rivers and associated wetlands, but their limited distribution and unique ecology set them apart from this general review.

MAMMAL COMMUNITIES

Quantitative data concerning relationships between mammals and wetlands are limited, and few comprehensive studies of wetland ecosystems provide more than qualitative descriptions of commonly observed species. For this study, I will selectively emphasize

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mammalian communities in North American freshwater wetlands, mainly because of their familiarity to me and the accessibility of published and unpublished information.

Three regional wetland types were chosen to illustrate mammalian communities because they differ markedly in character and are geographically separated.

- (1) Prairie potholes are small, closed, shallow basins well-inter-spersed among grasslands and parklands in the central portion of the continent (Stewart and Kantrud, 1971). Seasonal and annual changes in water levels and muskrat activity influence the predominant aquatic vegetation pattern (van der Valk and Davis, 1978a).
- (2) Northeastern bogs and fens are wetlands within the boreal forest of northeastern North America. They include peatlands with a high water table in closed or nearly closed basins. Vegetative cover is characterized by mosses (primarily Sphagnum), sedges, ericaceous shrubs, and coniferous trees (Zoltai and Pollett, 1983).
- (3) Bottomland hardwoods are wooded wetlands associated with rivers and streams in the southeastern United States. Seasonal flooding of varying depth and duration influences the structure of the diverse deciduous forest community (Fredrickson, 1978; Clark and Benforado, 1981).

Description of each community and niches of each species were based on reviews of mammals in wetland ecosystems (Fredrickson, 1978; Handley, 1979; Wharton, Lambou, Newsom, Winger, Gaddy and Mancke, 1981; Larsen, 1982; Harris and Vickers, 1984) and synthesis of information from regional works on mammals (Banfield, 1974; Lowery, 1974; Godin, 1977; Sealander, 1979; Wrigley, Dubois and Copland, 1979; Hazard, 1982; Jones, Armstrong, Hoffmann and Jones, 1983; Pendleton, 1984). Delinement of wetland mammals communities was based on Eisenberg's (1981, p. 248) ecological classification of mammalian substrate use and dietary specialization.

The three distinct wetland types examined all support assemblages of mammals occupying diverse niches, with 9-12 substrate/feeding specializations represented in each. Semi-aquatic forms are not common compared to other substrate specialists. Most wetland mammals that exploit resources found in wetland environments are adapted equally well to exploit other environments (Table 18.1).

Differences among the mammal communities of the three wetland types are perhaps more apparent than similarities. Prairie potholes clearly support fewer mammal species ($n = 18$) than do either northeastern bogs and fens ($n = 29$) or bottomland hardwoods ($n = 28$). The presence of woody vegetation in the latter two wetland types accounts for most of the disparity. Scansorial (climbing) mammals are absent from the treeless prairie potholes but account for three 'new' species in bogs and fens and four in bottomland hardwoods. The addition of one to three species of

browsing herbivores to the wooded wetlands also contributes to the differences in diversity.

The numbers of small insectivore/omnivore mammals is also lowest in prairie potholes with only two species, whereas seven species are found in northeastern bogs and fens (although short-tailed shrews, Blarina brevicauda, and smokey shrews, Sorex fumeus, do not range throughout the region) and four inhabit bottomland hardwoods. The relatively constant, high soil moisture associated with bogs and fens and bottomland hardwoods probably insures suitably friable soils for the fossorial moles and their prey. Shrews reach their greatest diversity and abundance where moisture levels in microhabitats remain relatively high (Wrigley et al., 1979). Periodic drought may preclude successful colonization of prairie potholes by insectivore/omnivores except for the widely distributed short-tailed shrew and masked shrew (S. cinereus), which are able to inhabit xeric habitats (Wrigley et al., 1979).

Mammals are generally distributed in wetlands in relation to water levels and the associated vegetative communities. In prairie potholes, small mammals were found to select habitats based on soil moisture levels (Pendleton, 1984). Meadow voles (Microtus pennsylvanicus) were most commonly associated with moist sites, and deer mice (Peromyscus maniculatus) predominated at drier sites. Masked shrews and short-tailed shrews were found in transitional habitats intermediate in moisture. The distributions of other small mammal communities in bottomland hardwoods (Fredrickson, 1978) and Czechoslovakian marshes (Pelikan, 1978) also appear to be related to water levels and associated vegetative zones.

MAMMALS AND ECOSYSTEM DYNAMICS

Although no large taxon of mammals has radiated to occupy wetland environments (such as the avian families, Anatidae, Rallidae, Scolopacidae and others) numerous species on every major land mass have become wetland specialists. A review of Walker's Mammals of the World (Novak and Paradiso, 1983) reveals a variety of specialized mammals occupying diverse niches in swamps, marshes and other wetland types (Table 18.2). Other semi-aquatic forms inhabit wetlands, but are also commonly found in lakes, streams and rivers. Many more 'terrestrial' mammals exploit wetlands opportunistically as part of a larger habitat base.

Few comprehensive studies of wetlands have incorporated mammals into quantitative analyses of ecological processes. This may be a result of the relative unimportance of mammals to annual productivity in most systems. The most complete analysis is that of Pelikan (1978) who assessed the energy budget of a mammal community in managed Czechoslovakian wetlands. The amounts of energy fixed annually in secondary production of mammals were: 4.68 kcal/m² for herbivores (primarily muskrats, Ondatra zibethicus), 0.15 kcal/m² for insectivores and 0.014 kcal/m² for carnivores. Collectively these values were about half the productivity of birds in the same ecosystem (Hudec and Stastny, 1978). The greatest effect of mammals, however, was through their

Table 18.1: Mammals associated with three North American regional wetland types classified by substrate utilization and feeding adaptations

	Prairie potholes	Northeastern bogs & fens	Bottomland hardwoods
<u>Fosorial</u>			
Insectivore/omnivore	<u>Condylura cristata</u>		
<u>Semifosorial</u>			
Frugivore/granivore	<u>Spermophilus tridecemlineatus</u> <u>S. franklinii</u>		
<u>Semiaquatic</u>			
Piscivore		<u>Lutra canadensis</u>	
Insectivore/omnivore		<u>Sorex palustris</u>	
Herbivore/browser	<u>Castor canadensis</u>	<u>Castor canadensis</u>	
Herbivore/grazer	<u>Ondatra zibethicus</u>	<u>Ondatra zibethicus</u>	
<u>Terrestrial</u>			
Carnivore	<u>Vulpes vulpes</u> <u>Mustela frenata</u> <u>M. nivalis</u> <u>M. vison</u>	<u>Canis lupus</u> <u>Felis lynx</u> <u>Mustela erminea</u> <u>M. nivalis</u> <u>M. vison</u> <u>Martes pennanti</u>	<u>Canis rufus</u> <u>Urocyon cinereoargenteus</u> <u>Mustela frenata</u> <u>M. vison</u> <u>Felis rufus</u>
Insectivore/omnivore			
	<u>Sorex cinereus</u> <u>Blarina brevicauda</u> <u>Mephitis mephitis</u>	<u>Sorex longirostris</u> <u>S. fumeus</u> <u>S. arcticus</u> <u>Microtus hoyi</u> <u>Blarina brevicauda</u> <u>Mephitis mephitis</u>	<u>Blarina brevicauda</u> <u>Cryptotis parvus</u> <u>Mephitis mephitis</u>

Table 18.1 (continued)

Frugivore/omnivore	<u>Procyon lotor</u>	<u>Ursus americanus</u>	<u>Didelphis virginiana</u>
		<u>Ursus americanus</u>	<u>Ursus americanus</u>
		<u>Procyon lotor</u>	<u>Procyon lotor</u>
Frugivore/granivore	<u>Zapus hudsonius</u> <u>Reithrodontomys megalotis</u> <u>Peromyscus maniculatus</u>	<u>Peromyscus maniculatus</u> <u>Zapus hudsonius</u>	<u>Oryzomys palustris</u> <u>Peromyscus leucopus</u> <u>P. gossypinus</u>
Herbivore/browser	<u>Odocoileus virginianus</u>	<u>Lepus americanus</u> . <u>Phenacomys intermedius</u> <u>Alces alces</u> <u>Rangifer tarandus</u>	<u>Sylvilagus aquaticus</u> <u>S. palustris</u> <u>Odocoileus virginianus</u>
Herbivore/grazer	<u>Microtus pennsylvanicus</u> <u>Bison bison</u>	<u>Clethrionomys glareolus</u> <u>Microtus pennsylvanicus</u> <u>Synaptomys cooperi</u> <u>S. borealis</u>	<u>Sigmodon hispidus</u> <u>Microtus pinetorum</u> <u>Synaptomys cooperi</u>
Scansorial Carnivore		<u>Martes americana</u>	<u>Sciurus carolinensis</u>
Frugivore/granivore		<u>Tamiasciurus hudsonicus</u> <u>Glaucomys sabrinus</u>	<u>Glaucomys volans</u> <u>Ochrotomys nuttalli</u> <u>Neotoma floridana</u>

Notes: a, Southern portion only
 b, S. cooperi found in southern portion of region, S. borealis in northern portion
 c, S. aquaticus found in western portion of region, S. palustris in eastern portion

Source: After Eisenberg (1981, p. 248)

Table 18.2: Selected 'wetland specialist' mammals

Order	Common name	Scientific name	Range	Foraging niche
Marsupalia	Quokka	<u>Setonix brachyurus</u>	SW Australia	Herbivore
Insectivora	Rice tenrecs	<u>Oryzorictes</u> spp.	Madagascar	Insectivore
	Web-footed tenrec	<u>Limnogale</u> <u>mergulus</u>	Madagascar	Insectivore/carnivore
	Russian desman	<u>Desman</u> <u>moschata</u>	SW USSR	Insectivore/carnivore
Lagomorpha	Swamp rabbit	<u>Sylvilagus</u> <u>aquaticus</u>	S. Central USA	Browser
Rodentia	-	Cabreramys obscurus	Uruguay	Herbivore/insectivore
	Water rat	<u>Scapteromys</u> <u>timidus</u>	Central S. America	Insectivore
	Web-footed rats	<u>Holocephalus</u> spp.	S. America	Herbivore
	Round-tailed muskrat	<u>Neofiber</u> <u>alleni</u>	Florida, USA	Herbivore/grazer
	Congo forest mouse	<u>Deomys</u> <u>ferrugineus</u>	West central Africa	Insectivore
	African water rat	<u>Colomys</u> <u>gosslingi</u>	Central Africa	Insectivore
	Big-eared swamp rats	<u>Malacomys</u> spp.	Central Africa	Granivore/insectivore
	Shaggy swamp rats	<u>Dasyurus</u> <u>incomtus</u>	Africa	Herbivore
	Falsewater rat	<u>Xeromys</u> <u>myoides</u>	NW Australia	Insectivore/carnivore
	Beaver rats	<u>Hydromys</u> spp.	Australia region	Insectivore/carnivore
	Capybara	<u>Hydrochaeris</u> <u>hydrochaeris</u>	S. America	Grazer
	Nutria	<u>Myocastor</u> <u>coypus</u>	S. America	Grazer
	Cane rat	<u>Thryonomysswinderanus</u>	E. Africa	Herbivore
	Giant otter	<u>Pteronura</u> <u>brasiliensis</u>	E. South America	Piscivore
	Otter clivet	<u>Cynogale</u> <u>bennettii</u>	SE Asia	Carnivore/omnivore
	Fishing cat	<u>Felis</u> <u>viverrinus</u>	SE Asia	Carnivore
Carnivora				

Table 18.2 (Continued)

<u>Artiodactyla</u>	<u>Hippopotamus</u> <u>Pygmy hippopotamus</u>	<u>Hippopotamus amphibius</u> <u>Choeropsis liberiensis</u>	Africa
Marsh deer		<u>Blastocerus dichotomus</u>	W. Africa
Sitatunga		<u>Tragelaphus spekii</u>	South America
Water buffalo		<u>Bubalus bubalis</u>	Central Africa
Nile lechwe		<u>Kobus megaceros</u>	S.E. Asia
Lechwe		<u>Kobus lecheve</u>	N.E. Africa
			S. Africa

Source: Novak and Paradiso (1983)

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consumption and structural modification of vegetation. Muskrats annually consumed or destroyed an estimated 5-10 per cent of the net above-ground production of Typha and other rodents destroyed 2.2-2.9 per cent.

In the marshes of the North American prairie, muskrats are also considered to play a significant ecological role. Prairie marshes exhibit a cycle of vegetative change lasting 5 to 30 years, depending on precipitation and resulting water level changes (Weller and Spatcher, 1965; Weller and Fredrickson, 1973; van der Valk and Davis, 1978a). Within this cycle, muskrat populations respond to changes in the abundance of emergent vegetation, primarily Typha. Muskrats affect the structure of the marsh vegetation by the intensity and pattern of their foraging and lodge-building activities. Subsequent changes in primary production (van der Valk and Davis, 1978b), decomposition rates (Davis and van der Valk, 1978), invertebrate communities (Voights, 1976; Kaminski and Prince, 1981) and bird populations and communities (Weller and Spatcher, 1965; Weller and Fredrickson, 1973; Murkin, Kaminski and Titman, 1982) are all thought to be influenced by muskrat activity. The effects of other semi-aquatic grazing mammals, such as the capybara (Hydrochaeris hydrochaeris), round-tailed muskrat (Neofiber alatus) and nutria (Myocastor coypus), are yet to be quantified in other wetland systems.

The roles of insectivores and carnivores in the dynamics of ecosystem processes are poorly known. Insectivores, however, may be especially important in regulating invertebrate communities in some wetland systems. The abundance and diversity of invertebrates associated with detrital-based food webs in wetlands would seem to provide excellent resources for exploitation by insectivorous mammals. Insectivory is a common foraging niche among small wetland specialists (Table 18.2), and important ecological relationships may be revealed as some of these species are studied in detail.

WETLANDS AS HABITAT FOR MAMMALS

Although the value of most mammals to the functioning of wetland ecosystems is not well understood, the value of wetlands as habitat for mammals is clear. Many mammals obtain important resources from wetlands around the globe. Based on the relative contribution of wetlands to the food and cover requirements of particular species, the wetland mammals of a region can be placed in one of three categories:

- (1) Limited - those species for which wetlands are an essential habitat. Wetland loss will eliminate use of the area by the species.
- (2) Influenced - those species for which wetlands are an important source of food and/or cover. Wetland loss will decrease carrying capacity but not eliminate the use of the area by the species.

- (3) Unaffected - those mammals which regularly use wetlands, but for which wetlands are unnecessary for food or cover. Wetland loss is not likely to decrease carrying capacity and may increase it.

The three wetland mammal communities described earlier have been classified in Table 18.3.

Species limited by the availability of wetland habitats include those for which wetlands provide the sole source of food and cover, such as muskrats in the otherwise waterless prairies or swamp rabbits (Sylvilagus aquaticus) in the southeastern United States. Without marshlands, muskrats might be able to survive in the few small streams or lakes on the prairie, but their existence would be tenuous. The importance of wetland habitat to swamp rabbits has been demonstrated by the concomitant declines of the species and bottomland hardwoods in Missouri (Korte and Fredrickson, 1977).

Mammals influenced, but not limited, by the availability of wetland habitats include species which benefit from food and cover provided by wetland habitats but whose populations would remain viable without those resources. Populations of these species may reach their highest densities in wetlands. Perhaps the best example is the direct relationship between moose (Alces alces) and wetland vegetation on Isle Royale (Belovsky and Jordan, 1981). Able to meet only 7-14 per cent of their sodium requirements by consuming terrestrial vegetation, moose turn to sodium-rich aquatic macrophytes during the summer. Moose then retain enough sodium to avoid deficiency and to support subsequent growth and reproduction during the rest of the year. Belovsky and Jordan (1981) concluded that 'a relatively small decline in aquatics could have a major impact on the herd,' a relationship supported by modeling (Belovsky, 1981). Because moose may sometimes consume close to 100 per cent of the available aquatic macrophytes at a site, the impact of their activity on wetland structure and function would appear to be significant.

Numerous mammals are able to use and colonize wetlands because these habitats meet all or parts of their broad niche requirements. Yet events that destroy the 'wetland character' of the area (such as drainage) do not necessarily lower its value to the species. These unaffected species may be among the most common mammals in an area. In comparing floodplain and upland populations of the ubiquitous white-footed mouse (Peromyscus leucopus), Batzli (1977) demonstrated that regular, prolonged flooding had little impact on their populations. Although population densities in the floodplain fluctuated more than those in the adjacent uplands, no other differences in demography were detected. He even suggested that the floodplain population may have served as a source of recruits for the upland. Although these mice are generally associated with mesic or xeric habitats, they function very well in some wetland communities. Their populations would not likely be affected by minor wetland modification or drainage. Unaffected species, such as white-footed mice, would serve as poor indicators of wetland loss or perturbation.

Table 18.3: Mammals of three North American wetland types categorized by the importance of wetland habitat

	Limited	Influenced	Unaffected
Prairie potholes	<u>Ondatra zibethicus</u> <u>Castor canadensis</u> <u>Procyon lotor</u> <u>Mustela vison</u>	<u>Sorex cinereus</u> <u>Blarina brevicauda</u> <u>Microtus pennsylvanicus</u> <u>Zapus hudsonius</u> <u>Vulpes vulpes</u> <u>Mustela frenata?</u> <u>Mustela nivalis?</u> <u>Mephitis mephitis</u> <u>Odocoileus virginianus</u>	<u>Spermophilus tridecemlineatus</u> <u>S. franklinii</u> <u>Reithrodontomys megalotis?</u> <u>Peromyscus maniculatus</u> <u>Bison bison</u>
Northeastern bog and fens	<u>Condylura cristata</u> <u>Sorex fumeus</u> <u>Sorex arcticus</u> <u>Sorex palustris</u> <u>Microtorex hoyi</u> <u>Ondatra zibethicus</u> <u>Castor canadensis</u> <u>Mustela vison</u>	<u>Sorex cinereus</u> <u>Blarina brevicauda</u> <u>Microtus pennsylvanicus</u> <u>Synaptomys cooperi?</u> <u>Synaptomys borealis?</u> <u>Phenacomys intermedius?</u> <u>Zapus hudsonius</u> <u>Lepus americanus</u> <u>Mustela erminea</u> <u>Mustela nivalis</u> <u>Alces alces</u> <u>Rangifer tarandus</u>	<u>Tamiasciurus hudsonicus</u> <u>Glaucomys sabrinus</u> <u>Clethrionomys gapperi</u> <u>Peromyscus maniculatus</u> <u>Canis lupus</u> <u>Felis lynx</u> <u>Ursus americanus?</u> <u>Martes americana</u> <u>Martes pennanti</u> <u>Mephitis mephitis</u>

Table 18.3 (continued)

<u>Bottomland</u>	<u>Sorex longirostris</u>	<u>Blarina brevicauda</u>	<u>Didelphis virginiana</u>
<u>hardwoods</u>	<u>Sylvilagus aquaticus</u>	<u>Cryptotis parvus</u>	<u>Scalopus aquaticus</u>
	<u>Sylvilagus palustris</u>	<u>Sigmodon hispidus</u>	<u>Sciurus carolinensis</u>
	<u>Oryzomys palustris</u>	<u>Microtus pinetorum</u>	<u>Glaucomys volans</u>
	<u>Peromyscus gossypinus?</u>	<u>Synaptomys cooperi?</u>	<u>Peromyscus leucopus</u>
	<u>Canis rufus</u>	<u>Ondatra zibethicus</u>	<u>Neotoma floridana</u>
		<u>Ochrotomys nuttalli?</u>	
		<u>Castor canadensis</u>	<u>Mephitis mephitis</u>
		<u>Urocyon cinereoargentatus</u>	
		<u>Felis rufus</u>	
		<u>Ursus americanus</u>	
		<u>Procyon lotor</u>	
		<u>Mustela frenata</u>	
		<u>Mustela vison</u>	
		<u>Lutra canadensis</u>	
		<u>Odocoileus virginianus</u>	

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CONCLUSION

Wetlands throughout the world help maintain diverse communities of mammals. Although relatively few mammalian species can be considered 'wetland specialists', some of these may have profound impacts on vital ecosystem processes. Conservation of wetlands will not only insure the survival of those species limited by wetland habitats, but also contribute to the welfare of the many other species influenced by wetland environments. The ecology of mammals within wetland ecosystems is poorly known relative to that in other environments. However, additional research may reveal important relationships among many mammals and their wetland environments.

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Chapter Nineteen

ENDANGERED, THREATENED AND RARE WETLAND PLANTS AND ANIMALS OF THE CONTINENTAL UNITED STATES

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INTRODUCTION

Of the endangered, threatened and rare taxa in the United States a large number are wetland dependent. Of the 188 animals federally designated, 94 or 50 per cent are wetland related. Of the 103 plants listed, 29 or 28 per cent are wetland dependent. Fish, mussels and birds represent the largest number of endangered and threatened animals. Of the estimated 2,500 plants still in need of protection it is estimated that 700 may be wetland related. Although over half our nation's wetlands have been lost, increasing awareness of the functional role of these liquid assets has somewhat slowed the pace of loss in recent decades. Wetland endangered and threatened species have benefited from this trend, as pointed out by Williams and Dodd (1979). Why should we be concerned about preserving rare or endangered species? The analogy by Ehrlich and Ehrlich (1981) of the aeroplane from which wing rivets are being removed is most relevant. The man removing the rivets assures the passengers they have nothing to worry about. Obviously, no sane person would board such a plane. As the authors state

The natural ecological systems of Earth, which supply these vital services, are analogous to the parts of an aeroplane that make it a suitable vehicle for human beings. But ecosystems are much more complex than wings or engines. Ecosystems, like well-made aeroplanes, tend to have redundant subsystems and other 'design' features that permit them to continue functioning after absorbing a certain amount of abuse. A dozen rivets, or a dozen species, might never be missed. On the other hand, a thirteenth rivet popped from a wing flap, or the extinction of a key species involved in the cycling of nitrogen, could lead to a serious accident.

In most cases ecologists cannot predict the consequences of the extinction of a single species, but can foresee the long-term results of rivet popping.

Along with indirect benefits in maintaining life-support systems such as nutrient cycling, maintaining air quality, providing a fresh water supply and aiding in pollution filtration, wetlands also

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represent a genetic library. Wetland plants also have direct potential benefits in the fields of agriculture and medicine. In addition, there is also the 'Right to Exist Principle' elegantly expressed by Ehrenfeld (1978):

because they exist and because this existence is itself but the present expression of a continuing historical process of immense antiquity and majesty. Long-standing existence in Nature is deemed to carry with it the unimpeachable right to continued existence.

This is called the 'Noah Principle - 'after the best-known practitioner of conservation in history'.

Natural factors contributing to extinctions include size of range, population size, degree of specialisation and location in the food web. Natural extinctions have been widespread since life began 3.5 billion years ago. Only 5-10 million of the 500 million species that may have existed during these billions of years persist. However, in the last hundred years the rate of extinction has greatly accelerated due to man's activities. Among the factors contributing to the loss of wetland species have been draining, filling and habitat alteration of wetlands and the introduction of alien and domestic species, hunting for commerce, sport and food, and pest control. Extinction rates worldwide are difficult to estimate since only 1.5 million of the Earth's organisms have been identified and there are still 5-20 million species, mostly insects, yet to be identified. The current extinction rate may be as high as one species per day. This chapter will attempt to update the present status of wetland-dependent endangered, threatened and rare taxa in the continental United States.

ENDANGERED, THREATENED AND RARE WETLAND TAXA

In 1973 the Endangered Species Act provided a mechanism through the Fish and Wildlife Service to identify endangered and threatened taxa and their critical habitats in the United States. An endangered species is one in peril of extinction throughout all or a significant portion of its range. Critically endangered implies that, like the red wolf and condor, it will probably not survive without human assistance. Threatened means any taxon that is likely to become endangered within the foreseeable future. Rare indicates that the species is not endangered at present, but at risk because of low numbers.

Although most States have inventoried their rare biota regional publications by Crow (1982) for New England and Mohlenbrock (1983) for the major regions of the United States further highlight the problem. Stuckey and Bartolotta (1977) list 95 wetland-dependent plant species, nine of which are extinct, and Kusler (1983) lists 84 representative animals. As indicated in Table 19.1, 29 or 28 per cent of the 103 plant taxa federally listed are wetland dependent (US Dept. Interior, 1986). Substantial data are available for listing another 894 plants and another 1,623 are possibly appropriate, totalling 2,517 (US Dept. Interior, 1985). Of

these 700 may be wetland dependent. Of the 188 animals designated, 94 or 50 per cent are wetland related. Although the fishes represent the largest number of animals listed, at least 251 taxa are considered endangered, threatened or of special concern (Deacon, Kobetich, Williams and Contreras, 1979). Among the amphibians 39 are considered in jeopardy (Bury, Dodd and Fellers 1980).

For the remainder of this chapter, I shall by region highlight certain of the biota in need of protection and some of the problems in preventing their extinction. I have adopted the six major regions used by Mohlenbrock (1983) - the Northeast, Southeast, North central, South central, Rocky Mt. Region and Far West.

Northeast (ME, NH, VT, MA, RI, CT, NY, NJ, DE, PA, MD, WV)

Among the few federally listed endangered plants in the Northeast, Furbish lousewort (Pedicularis furbishiae), a member of the snapdragon family, has probably generated the most interest. It was discovered by Kate Furbish in 1880 and considered extinct until 1976 when it was rediscovered along the St John River in Maine. The Dickey-Lincoln hydroelectric dam was also being planned along the St John and would flood half the 28 colonies. The plant is restricted to a 10 ft (3m) wide swath on the river terrace where the average annual high river flow occurs. Its presence appears to be dependent upon disturbance between the upper shrubby alder and herbaceous belts (Dyer, 1983). Listed as endangered in 1976, the lousewort's plight was highlighted nationally in 1977 by CBS newsman Charles Osgood in his unique prose (Mohlenbrock, 1983).

Table 19.1: Federally endangered and threatened wetland taxa in continental United States

Plants	Endangered 17	Threatened 12	Total 29 ^a	Total taxa designated 103	% Wetland taxa 28
Animals					
Mammals	7		7	35	20
Birds	16	1	17	25	68
Fishes	26	6	32	66	48
Reptiles	6	1	7	11	63
Amphibians	5	1	6	8	75
Insects	1	4	5	13	38
Mussels	20		20	30	66
Total animals	81	13	94	188	

Note: a, An additional 139 wetland-dependent plant taxa which have been identified as in need of protection will be published elsewhere

Source: US Dept. of the Interior, Fish and Wildlife Service, 1 Jan. 1986

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Although more than 20 rare wetland plants have been identified, the Estuarine Monkey Flower (Mimulus ringens var. colpophilus) along the estuaries of the St Lawrence and Coastal Maine is adapted to saline conditions. Its taxonomic status is still uncertain; it may be an ecophene rather than genetically distinct. The Heart-leaved Plantain (Plantago cordata) found along calcareous streams is locally present from the Northeast to the Midwest and south to Alabama. Its deep green heart-shaped leaves distinguish it from the common lawn plantains. Two wetland orchids, the Auricled Twayblade (Listera auriculata), associated with calcareous alluvial soils, and the Ram's-head Lady's slipper (Cypripedium arietinum), found in conifer swamps from New England to Minnesota, are also in need of protection. Two species are extinct - Old Veteran Rush (Juncus pereetus), originally found on Cape Cod in fresh to brackish sites, and the streamside Schwenitz's Waterweed (Elodea schwenitzii) from Pennsylvania.

Southeast (VA,KY,TN,NC,SC,GA,AL,FL,MS)

The southeastern States have a large number of rare and endangered taxa. Carnivorous plants are conspicuous among the threatened plants. Wet pine savannas and boggy areas contain a variety of insectivorous plants in need of protection. The Green Pitcher Plant (Sarracenia oreophila) is federally listed as endangered and the Canebrake Pitcher Plant (Sarracenia alabamensis), although not yet listed, is included in the IUCM Red Data Plant Book (1978), a worldwide listing of endangered species. Several other pitcher plants are also rare as is the Venus Fly Trap (Dionaea muscipula) which is being threatened by collecting, habitat destruction and forest encroachment. Site preparation for new pine plantations can destroy them and fire suppression can shade them out since these plants thrive best in openings. The Southern Yellow Orchid (Platanthera integra), a fringeless form currently under review, occurs in pitcher plant habitats.

Three other plants - Harper's Beauty (Harperocallis flava), a lily, Ruth's Golden Aster (Pityopsis ruthii) and the Bunched Arrowhead (Sagittaria fasciculata) are on the endangered list. The first, an endemic to the Apalachicola River Region, is known from only three locations. Only about 100 plants of Harper's Beauty persist. In this forest there are nine other endemics including the endangered Florida Torreya (Torreya taxifolia), a conifer reaching 18 m tall. Other woody species on the federal list in the Southeast include Chapman's Rhododendron (Rhododendron chapmanni) Miccosukee Gooseberry (Ribes echinellum), and Virginia Round-leaf Birch (Betula uber). The birch, found in 1914 along the Dickey Creek, Virginia, resembles sweet birch but its flowers and rounded leaves are different. Although listed in 1978, by 1980 only 20 of the original 40 plants survived in the wild since a few had died and several had been transplanted for research and propagation (Mohlenbrock, 1983). Two species of Lindera are also under review.

Two ferns - the Dwarf Polypody (Grammitis nimbata) and the Single-sorus Spleenwort (Asplenium monanthes) are rare. The former from North Carolina is under review and only occurs in one

locality on moss mats under waterfalls. The small tufted evergreen spleenwort found in North and South Carolina and Florida and disjunct to Arizona is restricted to cool shaded ravines near rivers or waterfalls.

Within this region four aquatics - the Nashville Waterweed (Elodea linearis), Florida Hornwort (Ceratophyllum floridanum), Water-hyssop (Bacopa simulans) and a Pondweed (Potamogeton floridanus) are reported as extinct (Stuckey and Bartolotta, 1977).

Over 30 animals are federally recognised as endangered or threatened in the Southeast. Among the mammals are the Florida Panther (Felis concolor coryi), Key Deer (Odocoileus virginianus clavium) and Florida Manatee (Trichechus manatus latirostris). The last, found in shallow fresh water, feeds on aquatics such as water hyacinth, one of its favourite foods. The manatees are easily injured by boat propellers and are also harrassed by swimmers. Two rare small mammals, the Dismal Swamp Southeastern Shrew (Sorex longirostris fisheri) and Silver Rice Rat (Oryzomys argentatus) in Florida are endangered by interbreeding and draining and filling of wetlands.

At least ten birds are in need of protection. The Everglade Snail Kite (Rosthrhamus sociabilis plumbeus), as a highly specialised feeder, depends solely on the apple snail whose habitat must also be preserved. The Wood Stork (Mycteria americana), primarily in Florida, is especially dependent on wetland pools for concentrating small fish during the nesting season. It has declined from 75,000 in the 1930s to 10,000 in 1979. This species has suffered greatly from drainage and wetland manipulation. Three spectacular wading birds need protection - the Mississippi Sandhill Crane (Grus canadensis pulla), which is endangered, and the Florida Sandhill Crane (Grus canadensis pratensis) and Florida Great White Heron (Ardea occidentalis occidentalis) which are threatened. In the early 1970s the annual kill of Mississippi Sandhill Cranes in Canada and the United States was between 10,000 and 12,500 or 5-6 per cent of the total population of 200,000. This exceeded annual recruitment of new individuals (Miller, 1974). In 1984 there were 82 birds remaining. Three song birds are federally listed - the Bachman's Warbler (Vermivora bachmanii), originally found nesting in dense forested wetlands and last reported in 1962 with sporadic sightings in 1975, the Cape Sable Sparrow (Ammodramus maritima marabilis) with a population of about 6,600 in 1981 and the Dusky Seaside Sparrow (Ammodramus maritima nigrescens) whose plight is more serious since only males have been observed.

Among the reptiles the American Alligator (Alligator mississippiensis) has made a remarkable recovery. Its status has been upgraded to threatened in Florida and parts of Georgia and South Carolina and endangered elsewhere. In addition to the alligator, the American Crocodile (Crocodylus acutus), associated with both fresh and saline habitats, is endangered with fewer than 500 individuals left. The young crocodile needs some exposure to salt water to survive. Therefore, water level manipulation has adversely affected this reptile. The marine Green Sea Turtle (Chelonia mydas) is also endangered and dependent upon aquatic beds of turtle grass in the shallow coastal waters of Florida. The threatened Atlantic Salt Marsh Snake (Nerodia fasciata taeniata),

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which is restricted to Florida, is one of few snakes adapted to saline conditions. The beautiful Pine Barrens Tree Frog (Hyla andersoni), ranging as far north as New Jersey, is especially threatened in the southern part of its range.

Several fishes, primarily darters, are endangered. The Snail Darter (Percina tanasi) is best known in conjunction with the construction of the Tellico Dam in Tennessee which was exempted from the Endangered Species Act by Congress. Fortunately, other populations of the darter were subsequently found outside the flooded area. Over 15 federally listed endangered mussels occur in the riverine systems of Virginia, Tennessee, Kentucky and Alabama.

North Central (OH,IN,MN,MI,WI,IL,IA,MO,ND,SD,NE,KA)

In the North central or Lake States region mussels are among the most important endangered species. Four are found in the Mississippi or other riverine systems such as the Wabash in Indiana and Illinois, Black River of Missouri and Detroit River in Michigan. Two secondarily wetland-dependent fishes - the Madtom (Noturus trautmani), a small catfish, and the Blue Pike (Stizostedion vitreum glaucum) - are found in the Big Dary Creek, Ohio and Lakes Erie and Ontario, respectively. The former is federally listed as endangered.

Among the ten or more plants in need of protection the Northern Wild Monkshood (Aconitum noveboracense) is federally listed as threatened and has a disjunct distribution from Wisconsin eastward to Iowa, Ohio and the Catskills of New York. It is threatened by human encroachment, including collecting. Two species under review are the Lake Iris (Iris lacustris), found almost exclusively along the north shores of Lakes Michigan and Huron, and the Prairie Fringed Orchid (Platanthera leucophaea), with large fragrant creamy-white flowers, restricted to wet prairies of Minnesota and North Dakota and ranging eastward with one station in Maine. In Kansas it is found only in the native tall grass prairie.

South Central (AR,LA,OK,TX)

In this region, Texas has the greatest number of taxa in need of protection. Among the federally listed plants Texas Wild Rice (Zizania texana), an 8 ft (2.4m) high aquatic perennial, is endangered and restricted to a small area along the San Marcos River, the McKittrick Pennyroyal (Hedeoma apiculatum), a mint, is a threatened endemic frequently found in limestone canyons along streams in Texas and New Mexico. Tourism and habitat alteration are further threats to both of these plants. At least a dozen other wetland plants are in danger throughout this region.

The Red Wolf (Canis rufus) is critically endangered and restricted to southeast Texas and southwest Louisiana. With the expansion of the coyote's range the reproductive barrier has been broken and the wolf is now hybridising with the coyote and losing its genetic identity. Isolated populations are being established in the Pacific Northwest and the Midwest and plans are also underway

to introduce the wolf into the pocosin of eastern coastal North Carolina.

Among the birds, the endangered Whooping Crane (Grus americana) and Eskimo Curlew (Numenius borealis) winter on the Texas coast. An estimated 1,300 Whoopers in the 1800s has declined to dangerously low levels of around 100 individuals. The coastal marshes of the Aransas Wildlife Refuge in Texas are their wintering grounds.

Of the amphibians, the Houston Toad (Bufo houstonensis) and San Marcos Salamander (Eurycea nana) are endangered and threatened, respectively. The toad is known from three counties in central Texas and the salamander from one spring pool on the San Marcos River. The endangered Texas Blind Salamander (Typhlonolge rathbuni) is restricted to cave water and deep wells. Capping wells, draining and over collecting are threats to this species.

Six species of fish are federally listed including the Fountain Darter (Etheostoma fonticola), Comanche Springs Pupfish (Cyprinodon elegans), Big Bend Gambusia (Gambusia gaigei) and Pecos Gambusia (G. nobilis), all of which use wetlands for feeding and protection.

Rocky Mountain Region (MT, ID, WY, CO, UT, NM, AZ)

Although numerous wetland plants are rare or endangered in this region, the only two federally listed are the Maguire Primrose (Primula maguirei), with six known populations in Logan Canyon, Utah, none with more than 100 plants, and a Sedge (Carex specuicola) growing on a Navajo Indian reservation in Arizona along a spring seep near Inscription House Ruin. The latter is endangered by grazing and water development.

The fishes are the most threatened with six federally listed. Of the several trout, the Apache or Arizona Trout (Salmo apache) occurs in clear mountain streams but has been almost totally exterminated by exotic trout. The Gila Topminnow Poeciliopsis occidentalis), found in the backwaters of the Gila River drainage, was once a common fish in the southern Colorado drainage. Efforts are being made to remove predators from isolated areas where it occurs.

The Mexican Duck (Anas diazi), a smaller darker version of the Mallard, is rare and restricted to the marshes of Arizona, New Mexico and Texas. In 1975 there were 450-650 of these non-migrating ducks in the United States.

Only one small population of the endangered Wyoming Toad (Bufo hemiophrys baxteri) occurs on private land in southeastern Wyoming. Breeding in temporary pools, it is threatened by drainage and pesticides, especially atrazine which is widely used on 'noxious weeds' along roadsides and field edges where the toad feeds. Fenthion, a pesticide used in mosquito control, is another hazard. Discovered in the Laramie Basin in 1946, this toad is thought to be a postglacial relict population.

The Great Basin Silverspot Butterfly (Speyeria nokomis nokomis) is found in two sites in western Colorado and is associated with spring fed meadows where its larval food is a wetlands violet.

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Far West (CA, NV, OR, WA)

This region has the largest number of federally endangered and threatened wetland taxa - 31 animals and 15 plants. In addition, more than 20 wetland plants have also been recognised as rare and possibly endangered. In Nevada and California there are two distinctive wetland ecosystems with a considerable number of endangered species. The desert springs of southern Nevada are maintained by several dozen springs or seeps fed by an aquifer of fossil water deposited more than 10,000 years ago. This area contains the largest concentration of endemic plants and animals in the United States. Seven plants, four pupfishes and one insect are currently federally listed and now protected at Ash Meadows in Nevada. This 11,000 acre preserve was initially purchased by The Nature Conservancy in 1984 (Schwartz, 1984) and then turned over to the Fish and Wildlife Service as a wildlife refuge. This unique area is comparable to the Galapagos in that different species have evolved different adaptations at various isolated springs. For example, the pupfishes have developed remarkable adaptations to high salinity, low oxygen and high temperatures in different habitats. One species can withstand salinities six times that of sea water and another temperatures of over 100°F and near freezing. How they can maintain osmotic balance under such arid conditions may have possible applications in kidney research (Ono, Williams and Wagner, 1983). The one-inch long beautiful blue Devil's Hole Pupfish (Cyprinodon diabolis), described as a new species in 1930, spends its entire life on a shallow 10 x 18 ft (3 x 5.4 m) limestone shelf that overhangs the deeper pool and eats amphipods, diatoms and protozoans (Ono et al., 1983). Any lowering of the water level due to over pumping nearby could bring about extinction of this species. Its population ranges from 100 to 400 individuals. The small endangered Ash Meadows Naucorid (Ambrysus amargosus), a flightless aquatic insect 6 mm long, has also been reported from one site and eight molluscs are candidates for federal listing.

Among the rare plants are the yellow Ash Meadows Sunray (Enceliopsis nudicaulis var. corrugata), a composite, and the Spring-loving Centaury (Centaurium namophilum), an 18 inch (45 cm) high annual gentian, as well as members of the rose, pea, carrot and goosefoot families.

The second unique wetland system is the vernal pools in the Central Valley of California in which the species must adapt to flooded and then gradually drying conditions (Robinson, 1986). Some of the plants have developed remarkable morphological adaptations for coping with this environment (Zedler, in press). The annual Solano Grass (Tuctoria mucronata) seed depends on flooding for germination and a symbiotic relationship with soil fungi. Initially the leaves float and as the pool dries up they begin to take on the appearance of regular erect grass leaves. The San Diego Mesa Mint (Pogogyne abramsii), also an annual, is uniquely adapted to life in a vernal pool. Its seed germinates with the first significant rainfall which may be important in terms of its reaching the surface of the water when inundation occurs. It also retains its seed which may reduce loss to seed predators, especially ants.

The Santa Cruz Long-toed Salamander (Ambystoma macrodactylum croceum) is also endemic to two of these pools and threatened by agriculture and development. Fortunately, the Santa Cruz Board of Supervisors has adopted zoning laws protecting its habitat. The Nature Conservancy has six preserves protecting these vernal pool wetlands. Their Tulare Vernal Pools, owned since 1960, has been designated a Natural Landmark.

The coastal wetlands of California also have their share of endangered species. Six species - the American Peregrine Falcon (Falco peregrinus anatum), California Brown Pelican (Pelecanus occidentalis californicus), Light-footed Clapper Rail (Rallus longirostris levipes), California Least Tern (Sterna antillarum browni), Belding's Savannah Sparrow (Passerculus sandwichensis beldingi) and Salt Marsh Bird's Beak (Cordylanthus maritimus ssp. maritimus), an annual plant in the snapdragon family, utilise southern California salt marshes (Zedler, 1984a). Cordylanthus (referring to its clubshaped flower) occurs only at the upper edge of the marsh where it can disappear without any disturbance of the habitat. Its phenology is timed with the winter rainfall stimulated by lower soil salinities (Zedler, 1984b). Seeds germinate in water up to about 10 ppt. This knowledge will be invaluable in any restoration efforts. In addition, the Salt Marsh Harvest Mouse (Reithrodontomys raviventris), California Black Rail (Laterallus jamaicensis coturniculus), California Least Tern, California Clapper Rail (Rallus longirostris obsoletus) and San Francisco Garter Snake (Thamnophis sirtalis tetrataenia) are dependent upon coastal wetlands. In the fresh water cattail-bulrush marshes the Yuma Clapper Rail (Rallus longirostris yumanensis) and Amargosa Vole (Microtus californicus scirpensis) are endangered taxa. Two of the several fishes federally listed in California which use wetlands for food and protection are the Owens River Pupfish (Cyprinodon radiosus) found in the Owens Valley and the Mohave Chub (Gila mohavensis) found in desert springs. The Black Toad (Bufo exsul) is rare and found in two springs in Inyo County.

Among the woody plants, Truckee Barberry (Mahonia sonnei) is a small evergreen shrub known as 'the phantom of the Sierras'. It was 'lost' for 90 years and rediscovered in 1973 by a high school biology student along the Truckee River. Two small patches exist. It was federally listed in 1979 but is threatened by collecting and changing land use (Mohlenbrock, 1983).

In Oregon and California the California Pitcher-plant (Darlingtonia californica) is highly restricted to the coastal region in wet meadows and sphagnum bogs and must be watched carefully in terms of habitat destruction.

Five insects - three beetles and two butterflies - are also endangered or threatened in various wetland habitats in California and on the Washington and Oregon coasts. They are the Delta Green Ground Beetle (Elaphrus viridis), Beller's Ground Beetle (Agonum belleri), the Valley Elderberry Longhorn Beetle (Desmocerus californicus dimorphus) and the Lotus Blue Butterfly (Lycaeides argyrognomon lotis) in California and the Oregon Silverspot Butterfly (Speyeria zerene hippolyta).

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FUTURE OUTLOOK

Protection of endangered, threatened and rare species is now a global movement. The Red Data Books of the International Union for the Conservation of Nature and Natural Resources have highlighted the problem of species extinction on a global basis. As has been emphasised at this symposium, there is a determined effort within the IUCN to protect wetlands worldwide, not just for the rare and endangered taxa they support but because human populations in developing countries depend directly on wetlands for their existence.

In the United States there is also increasing concern to protect the remaining wetlands. The 404 wetlands legislation as carried out by the Corps of Engineers is relatively effective and an earlier Executive Order under the Carter Administration also focused on the need for federal agencies to protect wetlands. The Endangered Species Act has been a tremendous mechanism to bring to public attention the critical issue of habitat protection and the need to regulate water manipulative projects, especially those that will adversely affect rare and endangered wetland species. Most States also have active programs to safeguard their rare and endangered species.

Private agencies such as the National Wildlife Federation, Sierra Club, National Audubon Society, Wilderness Society and The Nature Conservancy are also actively involved in public education, inventories and acquisitions of critical habitats. The Conservancy's Natural Heritage Program (Roush, 1985), operative in many States, has focused on rare and endangered ecosystems and many critical tracts of land have been acquired. Its role as intermediary in the Ash Meadows acquisition is a classic example of the part this national organisation is playing. Vice-President of Science, Dr Robert Jenkins reports that of the Conservancy's 3,098 natural areas, 48 per cent safeguard, at least in part, water-related natural systems (Jenkins, 1983). Another wetland project, Crystal River, Florida, is a critical series of warm springs on which the manatee are dependent during the winter. The Conservancy's 'Rivers of the Deep South Program' has concentrated on preserving the lower reaches of the country's six best remaining Gulf Coast rivers. Here over 100,000 bottomland hardwood riparian acres are being protected. Last year a list of aquatic sites in need of preservation was issued (Fenwick, 1985). The National Audubon Society was an early leader in saving wetland birds from being exploited to extinction by man. Its mature Corkscrew cypress swamp sanctuary is currently a critical habitat for the endangered Wood Stork. Another newly initiated effort to save our disappearing flora is the Centre for Plant Conservation in Jamaica Plain, Massachusetts. It indicates some 3,000 rare plants that may disappear before the end of the century. The aims of the Centre are to bring rare plants into cultivation before they become extinct, Long-term seed storage, stimulation of research on rare plants, provision of a computerised data base and a display of vanishing flora to the public. Cooperation with botanic gardens and arboreta throughout the country is being sought to implement its objectives.

The future for many rare plant and animal species may be bleak unless we act quickly to slow the pace of habitat destruction. Federal, State and public organisations are mobilising their efforts to help slow the losses but time is running out. The words of my friend and colleague E.O. Wilson seem most relevant.

The worst thing that can happen - will happen [in the 1980s] - is not energy depletion, economic collapse, limited nuclear war, or conquest by a totalitarian government. As terrible as these catastrophes would be for us, they can be repaired within a few generations. The one process ongoing in the 1980s that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us. (Harvard Magazine, Jan-Feb 1980.)

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Chapter Twenty

AQUATIC INVERTEBRATES OF FRESHWATER WETLANDS: FUNCTION AND ECOLOGY

Henry R. Murkin and Dale A. Wrubleski

INTRODUCTION

Most research effort in wetland ecology to date has focused on economically important game animals, furbearers, and fish. Recent advances in our understanding of food chain support, nutrient cycling, and overall productivity of freshwater wetlands has drawn increasing attention to the importance of aquatic invertebrates in the ecology and function of these systems (Murkin and Batt, 1987). The objectives of this chapter are to review the biological values of aquatic invertebrates and to examine factors affecting invertebrate distribution and abundance in freshwater wetlands.

FOOD CHAIN SUPPORT

One of the most important values of aquatic invertebrates in freshwater wetlands is the role they play in food chain support (Murkin and Batt, 1987). Invertebrates are a critical link between the primary production/detrital resources of the system and the higher order consumers. The high level of aquatic macrophyte production in wetlands ensures that considerable plant material enters the system as detritus (Davis and van der Valk, 1978). The axiom 'freshwater marshes are detritus-based systems' is based on the concept that the trophic structure of wetlands proceeds from plant detritus, to micro-organisms, to a variety of invertebrate consumers, and then on to vertebrate consumers. This concept has been developed by analogy with streams (Vannote, Minshall, Cummins, Sedell and Cushing, 1980) and salt marshes (Odum and Heald, 1975) where invertebrates have been shown to be key factors in litter decomposition and secondary production. In spite of these widely held ideas, little information is available on the trophic status of wetland invertebrates or their role in the trophic dynamics of these systems.

Newly fallen plant litter is colonised by various microbes soon after it enters the water column (Berrie, 1976). These micro-organisms may actually increase the nutritive quality of the litter for secondary consumers (Valielia and Rietsma, 1984). Shredders or grazers are the first invertebrate groups to respond to large litter particles and their associated microbes. Amphipods and snails have

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been described as shredders and scrapers in freshwater wetlands (Nelson, 1982). These groups reduce the size of litter particles through their feeding activities. As particle size is reduced, the litter becomes available to different groups of consumers. Nelson and Kadlec (1984) suggest that transport of fine particulate organic matter may be one of the most important factors affecting invertebrate production in freshwater wetlands. Very fine particles are removed from the water column by filter feeders, while collectors gather small particles that have settled on the various substrate surfaces within the habitat. The Chironomidae, one of the dominant invertebrate groups in freshwater wetlands (Wrubleski, 1987), has members in both these functional groups (Merritt and Cummins, 1984).

Whereas vertebrates such as muskrats may have a major impact on wetland vegetation (van der Valk and Davis, 1978), invertebrates normally do not cause major destruction of vegetation in wetlands through their feeding activities (Murkin and Batt, 1987). One area of herbivory that has received little attention is the use of the various algal communities by feeding invertebrates. Algae production in wetlands can be quite high (Hooper and Robinson, 1976; Shamess, Robinson and Goldsborough, 1985) and although vertebrates do not apparently feed on algae to any great extent (Murkin and Batt, 1987), invertebrates feeding on algae may be an important path in food chains linking the products of primary production to higher-level consumers (Cattaneo, 1983).

An important step in wetland food chains is the use of invertebrates as food by vertebrate consumers. Waterfowl feeding on invertebrates has been well documented (Swanson and Meyer, 1973; Murkin and Batt, 1987). The protein requirements of waterfowl increase during the breeding season due to the demands of egg-laying and gonadal development (Krapu, 1979). High protein invertebrates are selected over lower protein plant foods by feeding birds during this period. Other nutrients critical for reproduction are also available through invertebrate foods. The high calcium requirement of breeding female ducks for egg-shell formation may be met by feeding on snails (*Gastropoda*) with their calcium-rich shells (Swanson and Meyer, 1973). Juvenile waterfowl also obtain a wide range of amino acids and other nutrients necessary for rapid growth and development by consuming invertebrates (Sugden, 1973). Recent work has also indicated that waterfowl may be feeding on invertebrates outside the breeding season. For example, wintering birds may increase their consumption of invertebrates during periods of feather molts to meet the protein demands of new feather growth (Heitmeyer, 1985).

Besides waterfowl, many other species of birds in freshwater wetlands feed on invertebrates. Most marsh birds do so at some point in the life cycle (Weller, 1981). For example, red-winged (*Agelaius phoeniceus*) and yellow-headed (*Xanthocephalus xanthocephalus*) blackbirds only feed on invertebrates during the breeding season (Snelling, 1968, Mott, West, DeGrazio and Guarino, 1972), whereas others like marsh wrens (*Cistothorus palustris*) feed on invertebrates throughout their entire life cycle (Kale, 1965). High invertebrate production in wetland habitats may also affect avian use of adjacent habitats. For example, on the wooded

ridge separating Lake Manitoba and the Delta Marsh, several insectivorous passerine birds nest in unusually high densities due to the availability of adult insects emerging from the marsh (Busby and Sealy, 1979).

Wetlands associated with lakes or streams provide important rearing and spawning habitats for many species of freshwater fish (Toner and Lawler, 1969; Clark, 1978; Weller, 1978). Most use of wetlands by fish is seasonal in accordance with oxygen and temperature conditions (Ferguson, 1958; Bennett, 1962). Some fishes, primarily fathead minnows (*Pimephales promelas*) and brook sticklebacks (*Culaea inconstans*), can tolerate low oxygen levels and high summer water temperatures associated with many wetlands (Klinger, Magnuson and Gallepp, 1982). These adaptations allow them to take advantage of the habitat and abundant invertebrate resources provided by wetlands year round. These fish may then serve as forage for fish that are less tolerant of low oxygen concentrations and use the wetlands on a more seasonal basis.

Besides fish and birds, amphibians, reptiles, and mammals also feed on invertebrates in wetlands. Anurans and salamanders feed extensively on wetland invertebrates. Snakes and turtles are opportunistic feeders and will take advantage of abundant invertebrate food resources in wetland habitats (Clark, 1978). Many mammals like shrews, foxes, skunks, minks and raccoons feed on invertebrates during forays into wetland habitats (Murkin and Batt, 1987). The wide array of consumers that feed on invertebrates in wetlands emphasises the critical value of invertebrates to food chain support in these ecosystems.

NUTRIENT CYCLING

Kadlec (1979) states that animals may play some role in wetland nutrient cycling but provides little discussion or evidence on this topic. Valiela and Teal (1978) in their review of nutrient dynamics in freshwater wetlands conclude that animals are not a major factor in nutrient pools or cycling. The most probable reason that wetland invertebrates are dismissed in any treatment of nutrient dynamics is that at any point in time they do not make up a significant portion of the overall nutrient pool especially when compared to other components like primary producers. Kitchell, O'Neill, Webb, Gallepp, Bartell, Konce and Ausmus (1979) have suggested that animals can influence nutrient cycling through a number of physical processes. Without being a major pool themselves, invertebrates may actually regulate nutrient movements through translocation or transformation of nutrients within the system. Translocation is the movement of nutrients within the ecosystem boundaries, while transformation is the changing of surface-volume ratios of various substrates in ways which affect nutrient cycling processes.

In freshwater marshes large pools of nutrients are stored in the sediments (Kadlec, 1979) and invertebrates may facilitate translocation of these nutrients into the overlying waters. For example, Gallepp (1979) documented phosphorus release from the sediments to the water column by chironomid larvae. The larvae

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consume detritus, and possibly algae within the sediments, and then release nutrients through excretion into the overlying water. With respect to nutrient loss from the system by invertebrate movements, two studies from lakes (Vallentyne, 1952; Paasivirta, 1974) suggest that emerging insects represent negligible losses of nutrients from these systems. Movement of nutrients from more eutrophic wetlands by high numbers of emerging insects requires investigation.

Parsons and de la Cruz (1980) found that in the marshes they studied grasshoppers ingested only 0.03 per cent of the net primary production, but they returned to the soil through uneaten clippings 2.5 times more than they ingested. As a result the grasshoppers accelerated the rate at which nutrients returned to the sediments and water.

Although the transport of nutrients, detritus, and invertebrates among salt marshes, estuaries, and adjacent marine areas has been suggested to have ecological implications to overall estuarine productivity (Nixon, 1980), export of nutrients and invertebrates from inland wetland systems to other habitats has not been examined.

Besides movement of nutrients, invertebrate feeding can reduce the particle size of plant litter (transformation), thereby making the nutrients and energy contained in the litter available to a broad range of trophic levels. The number of bacteria able to colonise a piece of detritus is a function of its surface area. Any change which affects the surface-volume ratios will certainly affect nutrient release from the litter particles (Fenchel and Jorgensen, 1977). As the various organic compounds within the detritus are digested through a series of consumers, the chemical structure of the detritus also becomes less complex.

Invertebrates may also affect decomposition and nutrient release through direct action on microbial populations. For example, consumption by invertebrate consumers can prevent overgrowth of fungal mycelia and thus maintain the fungal populations in a state of maximum sustained yield and by implication a higher rate of nutrient release (McBrayer, 1973). Barsdate, Fenchel and Prentki (1974) found a 10-fold increase in phosphorus cycling in detrital systems with protozoa grazers. The actual excretion by the protozoa was found to be minor, with the increase resulting from higher turnover of phosphorus in grazed than in ungrazed bacterial populations.

INVERTEBRATES AS PESTS AND VECTORS OF DISEASE

Although the aquatic invertebrates of wetlands have positive biological values, there are also negative aspects to their presence as far as humans are concerned. Among the invertebrates produced by freshwater wetlands are biting pests and potential vectors of disease. These include mosquitoes (Culicidae), 'no-see-ums' (Ceratopogonidae), horse flies and deer flies (Tabanidae). Mosquitoes are one of the most important pests and disease vectors produced by wetland habitats and considerable effort is expended to control them in areas of human habitation. Large areas of

wetlands have been drained to control mosquito-born malaria (see Chapter 1). Marsh management for waterfowl can result in the production of large mosquito populations (Fleetwood, Steelman and Schilling, 1978). Knowledge of pest species biology and proper management techniques can minimise production of mosquitoes and other pest groups in problem areas (Rees and Andersen, 1966).

Besides their perception as pests by human populations, aquatic invertebrates also serve as intermediate hosts and transmittal agents for a wide range of parasites and diseases affecting many wetland vertebrate species (Wobeser, 1981). Although wetland management practices have been suggested to control diseases like botulism (Rosen, 1971), further information is required on this aspect of wetland invertebrate biology.

FACTORS AFFECTING INVERTEBRATE DISTRIBUTION AND ABUNDANCE

Freshwater wetlands are both physically complex and spatially patchy environments. The abundance and diversity of aquatic vegetation present provides a wide range of microhabitats and food resources for aquatic macroinvertebrates (Clark, 1978). Thus the overall densities and variety of species present are often quite high.

Aquatic invertebrate community composition and diversity are dependent upon wetland vegetation dynamics (Reid, 1985). Voigts (1976) correlated major shifts in invertebrate community composition with vegetation succession in Iowa marshes. Wrubleski (1984) reported that removal of sago pondweed (Potamogeton pectinatus) by waterfowl feeding had a major impact on the chironomid community. Removal of the pondweed resulted in a loss of habitat for the smaller epiphytic species. A further example demonstrating the importance of habitat to wetland chironomids is described in Wrubleski and Rosenberg (1984). Expanded polystyrene foam, used to float emergence traps, provided an ideal substrate for two species of burrowing chironomids. Both species were not abundant in the natural substrates beneath the traps.

Studies on the habitat structure provided by wetland vegetation suggests that the more finely dissected the leaf structure, the greater the abundance and diversity of invertebrates present (Krecker, 1939; Dvorak and Best, 1982). This is due to the larger surface area available for colonisation. In the Delta Marsh, for example, highest abundances and diversity of chironomids were found in shallow water dominated by sago pondweed with its highly dissected leaves (Wrubleski, 1984). Areas of the marsh dominated by cattail (Typha spp.) and bulrush (Scirpus spp.), which have narrow linear leaves, had much lower abundances of chironomids.

Few examples exist on the effects of changing food supplies on invertebrate distribution and abundance. Murkin (1983) reported a decline in cladoceran numbers during prolonged flooding of marsh habitat. A concurrent study on algae on the same study area showed that planktonic algae levels also declined during the same period (Hosseini, 1986). Cladocerans, being primarily

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planktivores, may have declined in response to this drop in phytoplankton levels.

In many cases, both habitat structure and available food resources in combination are important to invertebrate populations. Murkin and Kadlec (1986) reported that during prolonged flooding of a series of experimental marshes, benthos densities generally increased in most habitats. This increase was primarily chironomids in the collector-gatherer functional groups. These groups may have been responding to the increased fine particulate organic matter that became available through decomposition of the aquatic macrophytes killed by the initial flooding. Prior to flooding, the open-water habitats were dominated by sago pondweed which decomposes very rapidly leaving little or no coarse litter on the substrate surface. In these former open-water sites, where there was no coarse litter or plant material available as habitat for burrowing or tube building, the chironomid densities did not increase. Even though food supplies were abundant, habitat was apparently lacking for chironomid colonisation in these sites.

It is through life history traits that both habitat structure and food availability influence the distribution and abundance of wetland invertebrates (Reid, 1985). The life history of an organism includes many features in addition to food acquisition and habitat selection. These features include method of birth, rate of growth, mode of locomotion, behaviour, length of life, method of reproduction, and response to environmental factors. Within a species, a unique combination of these morphological, behavioural, and physiological characteristics have evolved in response to the selective forces of a particular environment. Because hydrologic regime is a major factor of freshwater wetland system function, one would expect many life history traits governing an organism's distribution and abundance to be a direct response to wetland hydrodynamics.

The requirement of standing water throughout development limits the distribution of many aquatic invertebrates to marshes that remain flooded for long periods. For example, amphipods common to prairie potholes cannot survive without water (Pennak, 1978) and subsequently are found primarily in semi-permanent and permanent wetlands. Many Hemiptera and Coleoptera also overwinter in permanently flooded marshes. Their high mobility, however, allows these insects to disperse from permanent ponds in the spring to flooded temporary and seasonal basins (Fernando and Galbraith, 1973).

Some aquatic invertebrates possess adaptations which allow them to spend all or part of their life cycles in wetlands which dry annually. In order successfully to occupy seasonally flooded wetlands, organisms must be able to resist desiccation and the extreme environmental conditions during the dry phase, be able to detect the return of favourable conditions upon reflooding and be capable of rapid development (Wiggins, Mackay and Smith, 1980). Despite these demanding conditions, seasonal wetlands are noted for their high invertebrate densities. These habitats offer rich detrital food resources and limit predation to those predators able to withstand the rigors imposed by a seasonal water regime.

A recent study on the Delta Marsh showed that by permanently flooding a shallow pond that was seasonally flooded for only short periods in the spring there was a marked change in the invertebrate groups in the pond (Neckles, 1984). Of the nine major invertebrate taxa present in the pond prior to permanent flooding, five were negatively affected by the continuous flooding. All the taxa unaffected by continuous flooding overwintered in water as juveniles and adults. In contrast, four of the five groups reduced by flooding overwintered as drought-resistant eggs. Continuous flooding apparently prevents females from laying eggs in suitable habitats (e.g. *Aedes* mosquitoes) or prevents proper development of embryos within the egg (e.g. cladocerans).

RESEARCH NEEDS

Studies of wetland macroinvertebrates are increasing, but we still lack important background information on the biology and ecology of these organisms. Many of the invertebrate species inhabiting these systems have not been properly identified making simple surveys and species lists necessary before more detailed work can proceed. Life history information is lacking on many of the dominant groups. Data on fecundity, generation time, growth rates, and trophic status are necessary prerequisites for studies of secondary production and food chain support. Their role as both nutrient pools and regulators of nutrient movements also requires investigation. The response by wetland invertebrates to various habitat manipulations requires further study, especially as management of these systems for wildlife production and pest and disease control become more common.

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PART IV

FORMATION, CHEMISTRY AND BIOLOGY OF WETLAND SOILS

Chapter Twenty-one

SOIL FORMATION UNDER HYDROMORPHIC CONDITIONS

S.W. Buol and R.A. Rebertus

INTRODUCTION

Soil wetness has long been recognised as an important consideration in land use, and nearly every soil classification scheme has differentiated wet soils from dry soils (Smith, 1973). Wetlands imply wetness, that is water-saturated conditions that occur for at least part of the year. Soils developed in the presence of enough moisture to cause anoxia are termed hydromorphic. Contrasted with hydromorphic is the adjective hydric, which means to be characterised by, or require, an abundance of moisture. As such, hydric is usually used to describe a moist habitat or a vegetational physiognomy indicative of moistness, but not a soil changed by high water content.

In the US comprehensive soil classification system known as Soil Taxonomy (Soil Survey Staff, 1975), an aquic soil moisture regime is defined to differentiate hydromorphic soils from better-drained soils having udic, ustic, xeric, and aridic soil moisture regimes. The aquic soil moisture regime is defined as one in which the whole soil becomes saturated with water long enough for dissolved oxygen to become depleted and reducing conditions to occur. With the exception of organic soils, the histosols, soils with aquic soil moisture regimes carry the formative element aqu and are classified in taxa of aqualfs, aquents, aquepts, aquolls, aquox, aquods and aquults.

As a form of technical classification, drainage classes have been widely used to characterise the wetness of soils based on the depth and duration of a water-table. The drainage class is inferred from profile morphology. Very poorly drained soils have water-table at or near the surface for the greater part of the year and dark gray or black coloured surface horizons over gray-coloured subsurface horizons. Poorly drained soils have a water-table at or near the surface for a considerable part of the year and are dominantly gray throughout. Somewhat poorly drained soils have a water-table at or near the surface for a significant part of the year and have gray mottles that occur in the upper B horizon (Soil Survey Staff, 1951). These drainage classes correspond in general to soils having an aquic moisture regime. Well- and moderately well-drained soils lack an aquic soil moisture regime near the soil surface.

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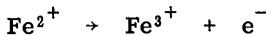
PHYSICAL AND CHEMICAL CHANGES UPON SATURATION

Water in soils is an agent of mineral weathering and is necessary to sustain plant life. It functions as the medium for the addition, translocation, and removal (leaching) of soil constituents. The temporal and spatial distribution of water in soil determines the rate of soil-forming processes and the chemical and physical environment for plant growth (Yaalon, 1983).

Saturated conditions in a soil usually result in the following physical and chemical changes (Buol, Hole and McCracken, 1980). (1) Redox potentials are lowered and reduction reactions predominate due to the replacement of oxygen from air-filled pore space and the slow rate of diffusion of gases in aqueous media compared to gaseous media. (2) Percolation, the downward movement of water and dissolved soil constituents, is restricted due to the high water-table. Lateral movement of water may or may not occur, depending on landform, relief and stratigraphy. As stated by Jenny (1941), 'the most active agency in soil-profile formation is percolating water. As long as water passes through the solum, substances are dissolved, translocated ... and the soil is not in a state of rest.' Where water remains in the soil for long periods of time, the removal of weathering products does not occur, thus retarding mineral weathering. (3) The heat capacity of the soil is increased and the soil tends to be cooler in the spring and warmer in the fall than surrounding, non-saturated soils. Onset of plant growth in the spring is thus postponed while warmer soil temperatures in autumn may result in a prolongation of the plant growing season. Daily soil temperature fluctuations near the surface are less in wet soils than in drier soils.

Redox Reactions

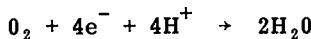
Oxidation occurs where oxygen supply is high or where biological demand for it is low. The most important oxidation reaction in soils is that of ferrous to ferric iron:



where e^- represents loss of an electron. In the high temperature and/or pressure environments in which primary minerals form, Fe is found only in the ferrous (bivalent) state. The oxidation of iron is one of the initial steps in the weathering of Fe-bearing primary silicates in low pressure-temperature near-surface environments. The change in ionic size and charge of ferrous iron as it is oxidised to ferric (trivalent) iron causes mineral structures to decompose. Nearly all primary minerals rich in iron are among the first to weather upon exposure to moisture in an oxidised environment. Important Fe-bearing primary silicates are biotite, chlorite, pyroxenes, epidote, and hornblende, and other amphibole group minerals. Release of iron from primary mineral structures is accomplished through a combined hydrolytic and oxidative reaction of the following type (Schwertmann and Taylor, 1977):



This reaction requires free oxygen to accept the released electron:

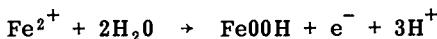


Reduction in soil environments occurs where water saturation occurs, oxygen supply of the saturating water is low, and biological oxygen demand is high. The presence of organic matter and sufficiently high temperatures to allow microbial activity results in biological oxygen demand. Oxygen serves as an electron acceptor allowing microbes to oxidise organic matter and obtain energy. Soon after water saturation of an initially aerobic soil, most oxygen is reduced by microorganisms. In acid soils, once oxygen is depleted, manganese is utilised as an electron acceptor at somewhat lower redox potentials, followed by nitrate, sulfur and finally iron. In soils of neutral and alkaline reaction, nitrate is reduced at a higher redox potential than is manganese (Bouma, 1983). Reduced Fe and Mn are mobile and will be leached if percolation is occurring. The reduced forms of nitrogen (N_2 , N_2O , and NO) are volatile and can be lost from the soil as gases.

The most common oxidation-reduction regime for hydromorphic soils is seasonal fluctuations in response to variations in weather. When a previously reduced soil becomes aerobic redox potentials rise, ferric and manganic oxides increase at the expense of ferrous and manganous oxides, and N and S oxidise.

Upon the return of water-saturated conditions, these reactions are reversed, and mobile, low oxidation state ions are produced which displace basic cations and exchangeable Al from cation exchange sites on clay minerals. Where deep percolation or lateral movement of water is occurring, these displaced cations are subject to leaching.

Subsequent reoxidation results in deprotonation, producing acidity:



In acid soils, in the absence of bicarbonate to neutralise the exchangeable hydrogen, the release of acidity may result in partial dissolution of clay minerals (Brinkman, 1970, 1977). However, in the absence of appreciable sulfur and iron, oxidation may cause no significant change in pH of the soil (Bloomfield, 1973), and therefore not result in significant decomposition of clay minerals.

Weathering under seasonally reduced conditions results in the interplay of two opposing forces which do not occur in permanently reduced or permanently oxidised soils. They are the slower rate of removal of the products of mineral weathering over that in freely drained soils, and the promotion of weathering resulting from hydrolysis upon reoxidation which does not occur in freely drained or permanently saturated soils. The result can vary depending on circumstances, but often little mineralogical difference is observed between oxidised soils and those having seasonally reduced conditions. The only difference is likely to be a lower crystallinity of clay minerals and a higher proportion of amorphous inorganic material in the seasonally reduced soils.

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Colour and Mottling

Colour is the most obvious soil characteristic and is readily determinable. A dark or black colour suggests the presence of organic matter, often indicating a poorly drained soil where decomposition of organic matter is impeded due to lack of oxygen. In the absence of appreciable organic matter, iron oxides determine the colour of most soils. The high surface area of iron oxides and their occurrence as coatings on other particles results in a strong pigmentary influence, even at low concentrations.

Red and yellow colours are indicators of oxidised iron, and hence aerobic conditions. Soils with red B horizons (redder than 5YR, Munsell notation) denote good aeration and usually occur on convex landscape surfaces underlain by pervious parent material (Soil Survey Staff, 1975). The red colour results from a significant hematite component, a non-hydrated iron oxide mineral (Bigham, Golden, Buol, Weed and Bowen, 1978). Yellow or yellowish-brown B horizons (5YR and yellower) are thought by many to indicate a somewhat moister, although still well-drained, condition than red colours. The hydrated iron oxide mineral goethite predominates in yellow-coloured soils. These soils are often thought to be more productive for plant growth than similar, associated red soils. Where both red- and yellow-coloured soils occur on the same landscape, their distribution is often indicative of hydrologic conditions near the surface. The yellow-coloured soils tend to occur on broader ridge tops or toeslopes whereas the redder soils usually predominate on narrow ridgetops and backslopes where water is less likely to perch temporarily during periods of high rainfall.

Mottled colour patterns result from the segregation of iron into zones as a result of different redox potentials, thus resulting in red, yellow, and gray mottled zones. Mottling is common in soils and usually indicates a fluctuating water-table of short duration. However, variegated or mottled colours may represent relict colours or differential weathering of minerals in compositional zones. The latter is quite common in parent materials.

Gray or whitish colours result where organic matter content is low and Fe has been reduced and leached to reveal the inherent colours of quartz and clay minerals. The gley colours, olive, bluish gray, and greenish gray, indicate the presence of appreciable ferrous iron. Gleyed soils result from periods of long saturation in which little water movement occurs through the soil, thereby preventing the removal of ferrous iron (Daniels, Gamble, Wheeler, Gilliam, Wiser and Welby, 1978). In such soils weathering and soil development have been virtually arrested in and below the gleyed horizons. Gleyed soils are usually associated with an aquiclude at shallow depth, often an impermeable geologic formation. The term gley is frequently used in the broader sense of indicating the presence of gray colours.

LOCATION, DYNAMICS, AND CLASSIFICATION OF HYDROMORPHIC SOILS

Four major settings resulting in hydromorphic soil formation can be identified. Two, broad upland plains and depressions, occur because of physiography or landscape position. A third type, restricted percolation, may result in a perched water-table within the soil profile regardless of landscape position. A fourth setting, occurring in tidal marshes, creates unique soil conditions and is often of extreme concern because of proximity to estuaries.

A fifth setting of soil saturation without reduction may occur but is not discussed. Lack of reduction in the presence of prolonged saturation has been reported where soil organic matter is absent or is too stable to provide an energy source for microbes (Daniels, Gamble and Buol, 1973; Bouma, 1983; Vepraskas and Wilding, 1983; Couto, Sanzonowicz and Barcellos, 1985).

Hydromorphic Conditions on Broad Upland Plains

On plains, such as those of the Atlantic Coastal Plain Province, depth to ground-water is largely controlled by depth of stream incision and by distance from the stream valley (Daniels, Gamble and Cady, 1971). Under this type of physiography, the rivers function analogous to drainage ditches in that the best-drained soils occur on the uplands adjacent to the river valleys. In the interior of the interstream divides, ground-water approaches the surface or may occur on the surface for extended periods of the year, particularly in the winter when evapotranspiration rates are low. Ground-water occurs nearer the surface for a greater proportion of the time where drainage divides are wide (Figure 21.1). Therefore, broad interstream divides have a greater proportion of soils with an aquic soil moisture regime. Where divides are narrow, ground-water is deeper (Figure 21.1). As the age of the geomorphic surfaces increases, the degree of stream dissection increases, streams become more numerous, and interstream divides narrow. Hence, the proportion of poorly and very-poorly drained soils decreases going from the younger, Lower Coastal Plain to the older, Upper Coastal Plain (Daniels et al., 1971), and there is a concomitant increase in well- and moderately well-drained soils.

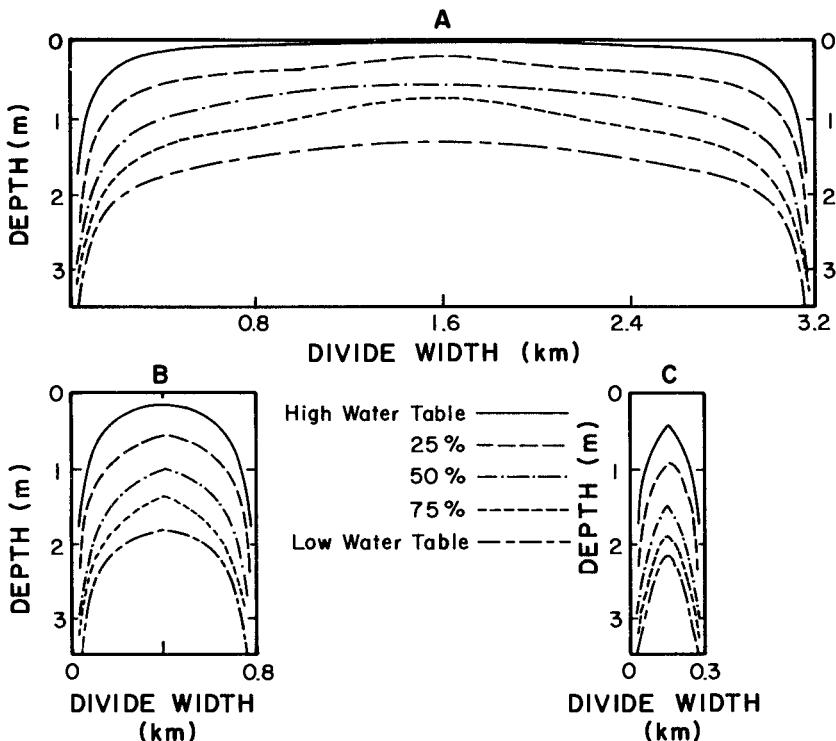
The poorly drained, hydromorphic soils formed in these conditions are most often very nutrient poor. As one can see by tracing the hydraulic gradients (Figure 21.1), all the subsurface flow of water is away from the centre of the divide. This scenario is most common for soils identified as Ochraquults and Paleaquults.

Where drainages are very widely spaced and little incised, removal of surface water may be so slow that annually produced organic matter does not completely decompose, and organic soils, histosols, develop. The histosols developed in such conditions are extremely acid and infertile (Dolman and Buol, 1967) because they develop where all the water flow is away from them. Over time the only nutrient input is from dust and rain water. Histosols produced in this way comprise highly decomposed organic material and have extremely low hydraulic conductivity (Boelter, 1965). Most of such histosols are identified as Typic Medisaprists if deep or

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Figure 21.1: Ground-water levels as a function of width of drainage divide: (a) a 3.2 km wide divide; (b) a 0.8 km wide divide; (c) a 0.3 km wide divide. The 25%, 50%, and 75% lines are saturation-time isopleths



Source: After Daniels et al. (1971)

Terric Medisaprists if shallow. It is important to identify the difference because the Terric Medisaprists can sometimes be drained for crop production if the underlying mineral soil is permeable. However, the deeper, Typic Medisaprists have slow subsoil permeability and are more difficult to cultivate adequately for crop use.

Hydromorphic Conditions of Depressions

Depressions in river valleys may hold flood or rain waters for periods long enough for reducing conditions to occur. The bottom of concave landforms on uplands may occur near or below the water-table and hence much of the soil may be saturated for part of the year. In addition to overland flow and direct precipitation, concave landforms may also receive interflow from higher areas.

Upon reaching the concavity, water movement ceases, water collects, and the water-table rises during periods of high precipitation or when evapotranspiration rates are low. Seeps may occur on backslope or footslope areas on the edges of the depressions and result in seasonal wetness.

Hydromorphic soils formed in depressions are subject to more diversity than those formed on broad flats. The most obvious process causing this is deposition from surface run-on. If the soil material eroded from adjacent uplands is fertile, the soil in the depressions tends to be very fertile. This can be observed both in micro positions along the flood plains of small streams and rivers below fertile fields, as well as in large flood plains and deltas of major rivers, such as the Mississippi, where fertile soil material from the head waters now forms the hydromorphic soils of the flood plain.

Rapid additions of soil material to the surface of a soil is usually evident by stratification of sediments. Such soils are classified as fluvaquents and fluvaquentic subgroups of aquepts.

Not as easily observed as surface deposition is the enrichment of depressions by subsurface flow of water. In geologically young parent materials such as glacial till or loess, weathering of primary minerals releases plant-essential nutrients. These ions find their way to the depressions via subsurface water flow. Also, the lateral subsurface flow becomes more saturated with silicon ions: thus the clays in the soils of the depressions are less weathered with higher cation-exchange capacity and base saturation than the clay fraction present in the surrounding uplands. As with other hydromorphic soils, organic matter contents are higher than in associated well-drained soils. Typical soils of this condition are the aquolls and aqualfs.

Hydromorphic Conditions of Restricted Percolation Sites

Several soil conditions can give rise to restricted rates of percolation in the subsoil. In fact, most soils have reduced permeability in their B horizons. When subsoil permeability is severely restricted, reducing conditions are created in the upper layers of the soil. Most frequently such conditions are caused by the presence of high contents of 2:1 type expandable clays (smectites) in the B or C horizon. The perched water-table effect is most pronounced in areas of abundant, but certainly not excessive, rainfall. This condition is frequently accompanied by an abrupt decrease in clay content above the clay-rich subsoil. Although the perched water-table is present long enough to create the necessary reducing conditions to qualify these soils as hydromorphic, it does not persist through dry periods. Plants are shallow rooted and tend to grow poorly because of too much water during rainy periods and too little water during dry periods. Although best characterised by albaqualls and albaquults (Soil Survey Staff, 1975), this condition is present to a lesser extent in several other kinds of fine-textured soils developed on nearly level upland positions.

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Hydromorphic Conditions of Tidal Marshes

A unique type of hydromorphic condition exists in the continuously saturated marshes bordering oceans, sounds, and tidal portions of rivers. Hydromorphic soils in tidal positions are so contrasting in dynamics from other hydromorphic soils previously discussed that they should be considered as separate soil systems (Daniels, Kleiss, Buol, Byrd and Phillips, 1984). These areas are subject to both occasional and regular inundation by fresh and brackish waters. Often the vegetative type is determined by the infrequent flooding with brackish water resulting from storms such as a hurricane. Between hurricanes the soluble salts are leached from the marsh soils by rainwater and/or tidal flooding with freshwater.

In some marshes, sediments have remained permanently saturated and have very low bearing capacity once the surface root mat is broken. Such soils are classified as hydraquents. Some of the clayey soils and some of the organic soils are commonly known as 'cat clays' or acid sulfate soils. Acid sulfate soils are an interesting group of hydromorphic soils in which there are appreciable amounts of sulfides close to the surface and few or no carbonates. Their genesis has been reviewed by Breeman (1982), Grossman (1983) and Pons, Breeman and Driessen (1982). They form in permanently saturated brackish coastal marshes where sulfate is reduced by bacteria to produce H_2S and HS. These compounds then react with Fe to produce insoluble iron sulfides. If the soils are then drained, extreme acidity is produced by the oxidation of the iron sulfide.

Acid sulfate soils are known as sulfaquents, sulfaquepts, sulfihemists, and sulfohemists. There are also sulfic subgroups of other soils where the sulfur content is deeper in the profile. Although highly distinctive, their occurrence is restricted to sediments that are deposited in coastal marshes and are not known to occur where marshes are protected from the open sea by barrier islands.

Because of their location, adjacent to the ocean, hydromorphic soils of tidal positions are unique among the larger category of hydromorphic soils. The exposure to frequent flooding, often by alternating fresh and brackish waters, leads to dynamics and characteristics that are difficult to generalize.

SUMMARY

The unifying process of soil formation under hydromorphic conditions is chemical reduction. However, there are several contrasting environments in which soil saturation and reduction can occur. Without identifying and understanding the factors and dynamics that give rise to individual kinds of hydromorphic soils, it is not possible to research, extrapolate or communicate information about them. Fortunately, the dynamics of the various classes of hydromorphic conditions can be generalised from a detailed soil classification system, such as Soil Taxonomy.

Information collected under the general categories of hydric or hydromorphic soil without attention to the specific setting of the site is of little value beyond the site where it was collected.

Generalisations regarding hydromorphic soils as a single group are misleading and erroneous.

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Chapter Twenty-two

CHARACTERISATION AND ORIGIN OF DELMARVA BAY BASIN FILL

M.H. Stoltz and M.C. Rabenhorst

INTRODUCTION

This study examined the characteristics and origin of basin fill sediments, and their effect on water-table fluctuations in Delmarva bays on the northern Delmarva Peninsula. The Delmarva Peninsula, composed of coastal plain sediments, separates Chesapeake Bay from the Atlantic Ocean. This peninsula is generally of low relief with elevations ranging from sea level to just over 30m. Extensive areas of swampy closed depressions surrounded by a distinct rim of sandy material (Delmarva bays) occur on the northern part of the Delmarva Peninsula. These are shallow depressions with changes in elevation generally 1.5 m from the top of the rim to lowest area of the basin. Bays range in length from 100 m to over 2 km. Depressions of this type are reported to occur along the Atlantic seaboard from New Jersey to Florida (Melton and Schriever, 1933; Johnson, 1942; Buell, 1946; Frey, 1951; Prouty, 1952; Rasmussen, 1958; Ingram, Robinson and Odum, 1959; Bryant, 1964; Savage, 1982), but are most extensively found in North and South Carolina where they are known as Carolina bays.

Organic matter, peat, or silty or clayey sediments have been reported to fill the basins of bays (Buell, 1946; Frey, 1951; Rasmussen, 1958; Ingram et al., 1959; Bryant, 1964). Ingram et al. (1959) concluded that the silty and clayey sediments were wind- or water-deposited Pleistocene sediments that had undergone little change since deposition. Rasmussen (1958) found that a continuous flow of ground-water was the primary contributor to the high water-table in bays in Delaware. Water-table gradients (the change in the elevation of the water-table over a given distance) were reported between 33 and 250 cm/100 m. The bays in Maryland are unique wetlands due to their seasonal flooding. These areas harbour many protected and rare plants.

The objectives of this study were: (1) to characterise the fine-textured sediments (basin fill) found in many of the bays; (2) to determine the effect of the basin fill on water-table fluctuations in the bays; and (3) to determine a probable origin of the basin fill.

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METHODS AND MATERIALS

A reconnaissance survey was conducted with the aid of black and white and infrared photographs, on the northern Delmarva Peninsula of Maryland during the summer of 1984 to identify representative types of bays. Soils were examined on the rim and in the basin of 53 bays. The 53 bays were grouped according to the nature of the basin sediments and were also characterised by shape, size, and soil-profile morphology. Six bays were chosen for detailed studies. At these six sites, soils were described (usually to a depth of 3.5m) at selected intervals along transects, from samples collected with a bucket auger, using the standard SCS procedures (Soil Survey Staff, 1981). Transects were from the top of the rim to the middle of the depression. Relief was determined using a rod and level.

In each of the three uncultivated study sites, five perforated PVC wells were installed at selected points along the transects from the top of the rim to the middle of the basin. The water levels in the wells were monitored at approximately 2-week intervals for a year. The volume of basin fill in several depressions was estimated by measuring elevations and thicknesses of those sediments at each point on a grid. Intervals between the grid data points were 20 m.

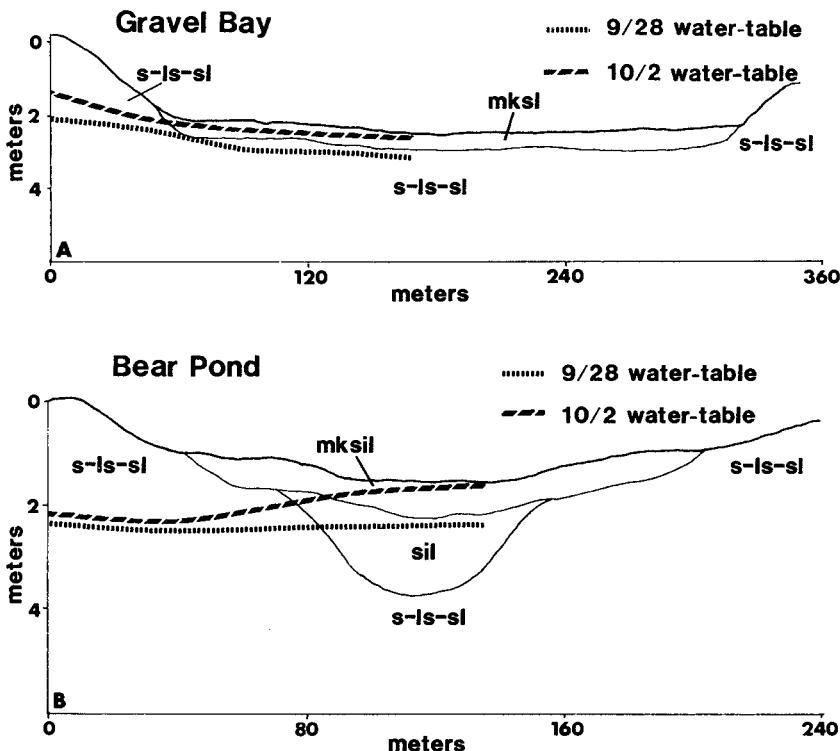
Laboratory analyses of the 2 mm size fractions performed on selected samples included particle size distribution (Kilmer and Alexander, 1949; Day, 1965), mineralogy (Jackson, 1956), and bulk density (Brasher *et al.*, 1966). Thin sections of selected horizons were examined using plane and polarised light microscopy.

RESULTS AND DISCUSSIONS

The reconnaissance survey indicated that two types of bay occur on the northern Delmarva Peninsula. The bays are differentiated by the presence or absence of substantial amounts of basin fill sediments of silt loam (sil) or silty clay loam (sicl) textures. Although most bays examined had at least a small amount of basin fill, deep areas of sil or sicl textured sediments occur in about 55 per cent of the bays. The thickness of these sediments is typically 1-3 m, but extends in some cases to over 5 m. The basins of the remaining 45 per cent of the bays examined were dominated by sandy parent materials.

Water-tables were monitored in the three wooded study sites named Bear Pond, Twin Bay and Gravel Bay. Although nearly 50 per cent of the 1985 precipitation occurred between 1 June and 30 Sept., the water-tables in all three bays were lowest in the late summer and fall. This probably indicates that the primary factor in the lowering of the water-table is evapotranspiration. Gravel Bay is the largest of the wooded depressions. The soil in the basin is primarily sandy with the basin fill sediments nearly absent. Gradients of the water table varied from 22 cm/100 m to 57 cm/100 m. The highest gradients occurred in the winter months when precipitation was greater than evapotranspiration, and the depression was filling up with water. Throughout the study period the water-table

Figure 22.1: Cross section of two Delmarva Bays and their associated water-tables before and after 7.3 cm of rain



always dipped from the rim toward the basin. Figure 22.1(a) shows the Gravel Bay water-table before and after 7.3 cm rain. Sand, sandy loam, and loamy sand textures dominate the soils of the rim and basin of this bay. The rim and basin soils have similar porosity, and therefore, fill at equal rates. Thus, following precipitation, the water-table shows little change in shape.

Water-tables for the other two wooded depressions were much different from that at the Gravel Bay site. Bear Pond and Twin Bay have sandy textured rims like Gravel Bay, but the basins are filled with substantial amounts of basin fill. These sediments appear to greatly affect the gradient of the water-table after a rainfall. Bear Pond is a small wooded depression with basin fill sediments approximately 2 m thick. The gradients of the water-table ranged from 0-40 cm/100 m toward the depression, to 0-30 cm/100 m away from the depression. During the fall, when the water-table was at its lowest level, the water-table rose faster in the depression than in the rim, following a rainfall. Figure 22.1(b) illustrates this change in water-table gradients after a 7.3 cm

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Table 22.1: Bulk density (BD), water content, and percentage available pore space at time of sampling of Twin Bay, and published bulk density and percentage water content by volume at 0.1 bar of tension for a Woodstown Sandy Loam

Horizon	Depth (cm)	BD (g/cm ³)	Water content (%)	Available pore space (%)
Twin Bay (basin soil)				
Oa	5-18	0.58	131.7	0
A1	18-40	0.91	50.3	0
A2	40-58	0.99	62.9	0
Bt1	58-75	1.59	27.7	0
Bt2	75-94	1.65	21.7	9.0
Bt3	94-160	1.42	40.0	0
Woodstown Loamy Sand (rim soil)				
Ap	0-25	1.39	18.4	29
Bt2	40-65	1.53	18.2	24

Source: White (1982)

Table 22.2: Particle size distribution and semiquantitative mineralogy of silt (2-50 µm) size fraction of selected Cg horizon basin fill samples

chl ^a	mica	qtz	fld	kln	PSD		
					sand (%)	silt (%)	clay (%)
Twin Bay							
x ⁺	X	XXXX	XX	X	20.6	66.8	12.6
Schribers Wallow							
x	X	XXXX	XX	X	13.8	66.4	19.9
Bear Pond							
-	-	-	-	-	8.3	71.7	20.0

Note: a, Abbreviations, chl = chlorite; qtz = quartz; fld = feldspar; kln = kaolinite; x⁺ = 5%; X = 5-10%; XX = 10-30%; XXX = 30-70%; XXXX = 70%; - = not determined

rain. A similar rise in the water-table was observed in the basin of Twin Bay after an autumn rainfall. The uneven fluctuation in the water-table between the rim and basin involves the texture difference in the soils of the rim and those of the basin. Bulk density and water content were measured in several horizons in the basin of Twin Bay. These samples were collected when the water-tables in this depression were at their lowest levels. Table 22.1 gives the bulk density and percentage moisture for the Twin Bay soil and the published values for Woodstown sandy loam, a typical rim soil. Using the bulk density and water content values (field moisture at time of sampling), the percentage available pore space was calculated for these horizons. The sil and sici sediments in the basins held much more water in their pores than the sandy rim soils even though the basin fill soils were at their driest stage. Under such conditions, when a rainfall event occurs, the remaining pore space in the unsaturated basin fill soil is quickly filled and the water-table responds by quickly rising. In the rim however, a larger pore volume must be filled in order for the water-table to rise.

Study sites Bear Pond, Twin Bay, and Schribers Wallow all contain substantial accumulations of basin fill. Table 22.2 gives particle size distribution (PSD) and mineralogy of representative basin fill sediments. These characteristics of the basin fill samples were almost identical, suggesting that these sediments are from the same or very similar sources. The silty basin samples were also very similar in mineralogy to nearby upland soils developed in loess. Foss, Fanning, Miller and Wagner (1978) reported that loess deposition on the eastern shore probably began around 10,000 YBP, and originated from the glacially influenced Susquehanna River and Chesapeake Bay.

The basins of Bear Pond, Twin Bay, and Schribers Wallow contain high n-value materials (materials with low bearing capacity) below a depth of 150 cm. The mean bulk density was 0.35 g/cm^3 and the mean n-value was 1.4. The high n-value and low bulk density of the sediments indicate that the materials have never been compacted and have probably remained saturated with water since their deposition. This sections of high n-value sediments showed no evidence of stratification suggesting that the sediments were deposited continuously or during one episode.

Foss *et al.* (1978) reported a decrease in loess thickness with increasing distance from the Chesapeake Bay. Based on this model, Delmarva bays further to the west (and thus closer to the Chesapeake Bay) should contain more basin fill. Our limited observations on estimated loess thickness for the study sites, however, did not show this trend. Evidence of loess deposited from the east has been reported in Pennsylvania.

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Chapter Twenty-three

GAS EXCHANGE AND ATMOSPHERIC PROPERTIES OF FLOODED SOILS

W. Stepniewski and J. Glinski

INTRODUCTION

Downward transport of oxygen in flooded soils is extremely difficult due to saturation of the soil with water. Compared to well-drained soils, there is a great difference in the depth of oxygenation and the consequences are of great practical importance.

In flooded soils, oxic metabolism occurs only in a thin oxygenated surface layer while in deeper horizons anoxic processes take place causing reduction of nitrates, Mn(IV) and Fe(III) oxides, and sulphates accompanied by H_2S and CH_4 production and CO_2 evolution.

The air evolving from paddy fields contains $0.01\text{--}0.20\text{ m}^3\text{m}^{-3}$ CO_2 , $0.10\text{--}0.95\text{ m}^3\text{m}^{-3}$ N_2 , $0.15\text{--}0.75\text{ m}^3\text{m}^{-3}$ CH_4 , and $0.00\text{--}0.10\text{ m}^3\text{m}^{-3}$ H_2 (Patrick and Mikkelsen, 1974). This wide variation is due to differences in the duration of flooding, soil and environmental conditions, microbial inhabitants and the nature of organic and inorganic substrates.

In this chapter the process of oxygenation of flooded soils as well as the formation and evolution of such gaseous products as CO_2 , CH_4 , N_2O , and N_2 are described.

OXYGENATION CONSUMPTION AND TRANSPORT

Well-drained soils take up oxygen and evolve equivalent amounts of carbon dioxide. The amounts of oxygen normally taken up by soils range from 0.1 to $10\text{ mg m}^{-3}\text{ s}^{-1}$, or, as related to unit soil surface, from 0.1 to $30\text{ dm}^3\text{ m}^{-3}\text{m}^{-2}\text{ day}^{-1}$ which corresponds to a cumulative uptake of $1.3\text{--}38\text{ mg ha}^{-1}\text{ yr}^{-1}$ (Glinski and Stepniewski, 1985).

The oxygen budget of flooded soils has been studied much less than that of the well-drained soils. When a soil is flooded its oxygen demand increases with time due to accumulation of reduced mineral compounds causing an increase in chemical oxygen demand which is normally negligible in comparison with microbial oxygen demand in well-drained soils. According to Patrick (1980), after two weeks of flooding the capacity to absorb oxygen increases to about 800 mg kg^{-1} . This implies high total oxygen demand in as much as chemical reactions are faster than biochemical ones (Ross

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and Potos, 1968). Reddy, Rao and Patrick (1980) found that flooded soils incubated under anoxic conditions after exposure to air consumed oxygen first in the process of chemical oxidation of Fe^{2+} and then (after several hours) both in the chemical and microbial oxidation processes. Grechin and Ignatiev (1968) found that soddy podzolic soil after 189 days of flooding in laboratory conditions, showed a 35-fold increase in oxygen uptake and an 8-fold increase in carbon dioxide production which suggests that most of the oxygen consumed was used in the chemical oxidation of reduced compounds formed during flooding incubation. This large oxygen demand is satisfied only after the flooding period is finished.

Oxygen diffusing into a flooded soil is consumed in a thin surface oxygenation layer as a result of microbial respiration as well as biological and chemical oxidation of reduced forms diffusing from the underlying reduced horizons. Not much is known about the relative contribution of these processes in the total oxygen uptake per soil surface unit. Howeler and Bouldin (1971) found that about 50 per cent of oxygen consumed by swamp soil was used in oxidising Fe^{2+} . Total oxygen uptake per soil surface unit is obviously lower than in well-drained soil causing a low rate of carbon mineralisation.

Oxygen is transported downwards in well-drained soils due to diffusion induced by its partial pressure gradients. Downward transport is further promoted in many situations by mass transfer caused by the occurrence of total pressure gradients due to diurnal variations of soil temperature, atmospheric pressure and periodical changes of ground-water level and soil moisture content.

When an unplanted soil is flooded, the downward transport of oxygen is caused solely by diffusion, except in the water layer stagnating on the surface which is subject to aeration by convection induced by temperature gradients and wind action.

Diffusion flow of any gas through a unit surface of the medium (f_x) is proportional to its partial pressure gradient (dP/dx) and the diffusion constant (K) of the medium, i.e.

$$f_x = -K \frac{dP}{dx} \quad (23.1)$$

The diffusion constant (K) in a partly saturated soil or any porous medium is related to the diffusion coefficient (D) as follows (Glinski and Stepniewski, 1985):

$$K = \frac{D}{RT} \frac{(Eg + B^0)}{Eo} \quad (23.2)$$

where R is the gas constant, T is absolute temperature, Eg is gas-filled porosity, 0 is volumetric water content, Eo is total soil porosity, B is Bunsen's solubility coefficient.

When the soil is saturated with water the K value is

$$K = \frac{D}{w} \quad (23.3)$$

where $2w$ is the gas solubility in water.

At 20°C the value of the oxygen diffusion constant in air K_o = 8.26×10^{-9} mol m $^{-1}$ s $^{-1}$ Pa $^{-1}$ and in water K_w = 2.87×10^{-14} mol m $^{-1}$ s $^{-1}$ Pa $^{-1}$ (Glinski and Stepniewski, 1985). It means that oxygen diffusion in water-saturated soil is about 300,000 times slower than in the air dry soil. Assuming that gas diffusion coefficient in dry soils ranges from about 2 per cent (for the most compacted soils) to 50 per cent (for the most porous ones) of its value in the free atmosphere we deduce that the K values for saturated soils are between 5.74×10^{-16} and 1.43×10^{-14} mol m $^{-1}$ s $^{-1}$ Pa $^{-1}$ (Glinski and Stepniewski, 1985).

The depth of oxygenation L in a homogeneous soil of uniform respiration rate (q) is given as follows (Glinski and Stepniewski, 1985):

$$L_{an} = \sqrt{\frac{2P_0 K}{2}} \quad (23.4)$$

where P_0 is the atmospheric oxygen partial pressure (20.7 kPa). This equation is valid also for vertical plant roots without radial oxygen losses.

The graphical interpretation of this relationship for the range of respiration rates in soils and in roots is presented in Figure 23.1. It can be seen that even for low soil respiration rates (0.1 mg m $^{-3}$ s $^{-1}$) oxygenation depth in water-saturated soils ranges from 2.5 to 14 mm depending on soil physical status. For higher respiration rates it decreases reaching values below 2 mm. This means that the possibility of increasing the oxygenation depth of flooded soils without plants is very limited. This is in agreement with the observed thickness of oxidised surface layers of paddy soils measuring usually several millimeters (Yu Tian-ren, 1980).

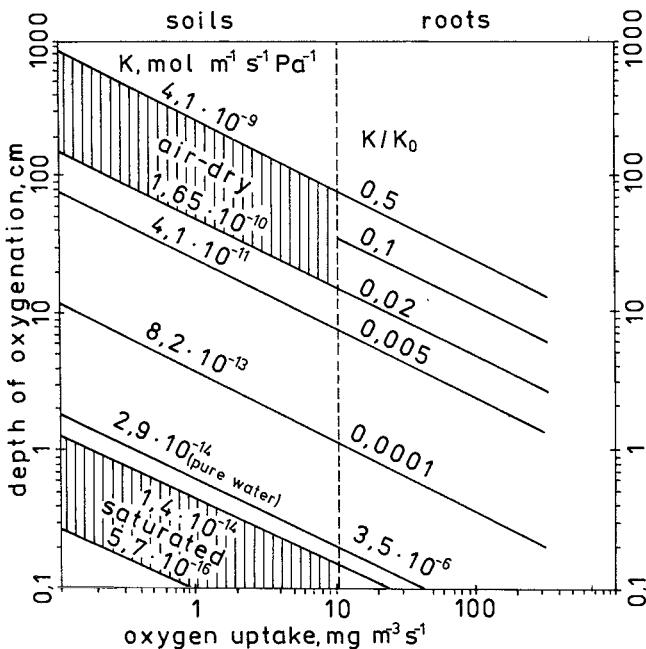
Several mathematical models describing oxygen distribution in the surface layer of flooded soils have been published by Bouldin (1968). Some of these models also include upward diffusion of reduced ions subsequently undergoing oxidation in the oxygenation layer.

In the presence of hydrophytic plants, downward transport of oxygen in flooded soils takes place mainly via their tissues (Armstrong, 1964, 1967, 1969; Jensen, Stolzy and Letey, 1967; Ando, Yishida and Nishiyama, 1983). It is generally accepted that the primary role in the oxygen delivery to the buried plant organs is played by diffusion. The contribution of mass transfer due to atmospheric pressure variation and soil temperature changes seems to be negligible. There are, however, special situations where mass transport may become of importance (see below).

Internal diffusion transport of oxygen is not dependent on the illumination of the plants (Ando et al., 1983). For many plants internal oxygen transport is sufficient not only to meet the oxygen demand of their roots but also to oxidise the surrounding soil (Armstrong, 1964, 1967, 1969; Ando et al., 1983, Holzapfel-Pschorn, Conrad and Seiler, 1986) which results in an increase in the soil oxygen level (Armstrong, 1964, 1967, 1969; Ando et al., 1983; Holzapfel-Pschorn et al., 1986) which leads to an increase in

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Figure 23.1: Soil oxygenation depth under steady-state conditions as a function of respiration rate calculated from equation (23.4)



Source: Modified from Glinski and Stepniewski (1985)

the redox potential of the rhizosphere to a depth of at least 30 cm (Yunkorvic, Smolyah and Sain, 1966; Holzapfel-Pschorn et al., 1986). Thus, plant-mediated diffusion transport appears to be the main factor of oxygen supply in flooded soils.

The importance of the mass flow of gases to plant roots has been recognised in two cases. In the first case Scholander, Dam and Scholander (1955) demonstrated the presence of mass flow in the pneumatophores of the black mangroves (*Avicennia nitida*). When the pneumatophores are flooded by the incoming tide CO_2 produced due to respiration of submerged plant organs results in a decrease of total gas pressure. As the tide recedes the under-pressure within the plant draws air into the pneumatophores. This phenomenon may occur in many plants although the flows seem to have limited physiological significance.

Another mechanism of gas exchange found in water plants is pressurised ventilation. This phenomenon was reported first in 1841 (Raffineau-Delile, 1841) in leaves of lotus (*Nelumbium*). Merget (1874) demonstrated the physical nature of this phenomenon in an experiment with dead lotus leaves, which after remoistening exhibited their capacity for pressurisation. Recently this phenomenon was studied in detail in yellow water lily (*Nuphar luteum*) by Dacey (1980, 1981). This plant, growing in lake sediments, has a

rhizome measuring several meters in length and up to 10 cm in diameter and several rosettes of leaves that rise up through the water on petioles which may be 2 m long. The plant has an extensive system of continuous gas spaces or lacunae occupying about 60 per cent of the petiole volume and up to 40 per cent of the volume of the roots and rhizome (Dacey, 1981). It was found that young leaves of the water lily show a small overpressure of up to 0.2 kPa. Due to this pressure several litres of air per day move down the petiole of the young leaves to the rhizome at a rate up to 50 cm min^{-1} and then up the petioles of the older leaves to the atmosphere. The overpressure in the young leaves is created by purely physical processes of thermal transpiration and hygrometric pressure induced by the temperature difference between the leaf and the atmospheric air. It occurs only during the day when solar energy creates the temperature differences (for details see Dacey, 1981). This mechanism obviously not only supplies oxygen but also removes methane and carbon dioxide from plant tissues (Dacey and Klug, 1979, 1982). It is not known how widespread this pressurised ventilation is among aquatic plants and further studies on this topic are necessary.

PRODUCTION AND EMISSION OF CARBON DIOXIDE

The content of carbon dioxide in the air of flooded soils and within the aquatic plants may reach 20 per cent (Patrick and Mikkelsen 1974; Dacey, 1980, 1981; Yoshida and Nishijama, 1983; Glinski and Stepniewski, 1985). Although carbon dioxide is produced in excess of the oxygen consumed, its total production under the flooded conditions is usually lower than in well-drained soils, as the mineralisation rate of organic carbon in anoxia is lower and some carbon is emitted to the atmosphere as methane. Kimura, Wada and Takai (1984) found that CO₂ production in a submerged soil within the rhizosphere of rice was quite stable ($4\text{-}6 \text{ mmol kg}^{-1} \text{ day}^{-1}$) and was determined by the physiological properties of the rice plants while non-rhizosphere soil evolved 1-2 mmol of CO₂ kg⁻¹ day⁻¹. Carbon dioxide formed in flooded soils is partly reduced to methane (Holzapfel-Pschorn et al., 1986), and is partly emitted to the atmosphere via the soil and/or via the plants (Higuchi, 1982; Yamakawa and Yamada, 1983; Holzapfel-Pschorn et al., 1986; Watanabe, 1986). In the latter case it can be partly or entirely assimilated in the plant shoots (Dacey and Klug, 1982; Smith, Wright and Patrick, 1983).

Diffusive transport of carbon dioxide in water-saturated soils is described by equation (23.1). The diffusion constant (at 20°C) for carbon dioxide in atmospheric air is $6.57 \times 10^{-9} \text{ mol m}^{-1} \text{ s}^{-1} \text{ Pa}^{-1}$ and in water $6.89 \times 10^{-13} \text{ mol m}^{-1} \text{ s}^{-1} \text{ Pa}^{-1}$ (Glinski and Stepniewski, 1985) which means that its diffusion in water is about 10,000 times lower than in air. Although the diffusion rate of carbon dioxide in air is somewhat lower than that of oxygen, in water-saturated soils it proceeds 24 times faster than diffusion of oxygen at the same partial pressure gradient. Nevertheless, diffusion through the soil is not efficient enough to remove all the carbon dioxide produced in the flooded soil, so it is emitted by

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ebullition together with methane and other gases. It was found that ebullition was very important in the unplanted field and in the presence of plant cover, internal transport via the plants dominated (Holzapfel-Pschorn et al., 1986).

Wada, Yokoyama and Takai (1983) found that upward diffusion $^{14}\text{CO}_2$, through the soil and through the floodwater was negligible in comparison to that through the rice plants. Of the total ^{14}C transported from the soil solution to the shoot about 70 per cent was fixed in the shoot under light conditions, but 100 per cent was recovered in the air under dark conditions. Carbon dioxide was transported through the rice plants together with the transpiration stream and by diffusion in the gas phase (Yamakawa and Yamada, 1983; Yokoyama and Wada, 1983; Watanabe, 1986) the latter factor being more important (Higuchi, 1982).

METHANE

Methane is an important gas evolving from flooded soils. Its tropospheric content is about 1.7 ppm in mid-northern latitudes (Cicerone and Shetter, 1981). Most of the atmospheric methane is produced biogenically; rice paddy fields, marshes and lakes are the most important sources (Dacey and Klug, 1979; Cicerone and Shetter, 1981; Feijtel, Delaune and Patrick, 1985; Sebacher, Harris and Barlett, 1985). The interest in methane production and evolution has been stimulated by its relation to stratospheric ozone content and to atmospheric temperature (Cicerone and Shetter, 1981). Methane content in the air bubbles evolving from flooded soils and in the air spaces within aquatic plants can reach 75 per cent (Patrick and Mikkelsen, 1974; Dacey and Klug, 1979; Sebacher et al., 1985).

According to Holzapfel-Pschorn et al., (1986) methane is produced by strictly anaerobic methanogenic bacteria which use only a limited range of substrates such as $\text{CO}_2 + \text{H}_2$ or acetate; the product of mineralisation of more complex substrates by other anaerobic bacteria.

Kimura et al., (1984) stated that methane in paddy fields is formed on and/or outside the roots and that formation is more active on the older than on the younger roots.

Methane is either released to the atmosphere or is oxidized to CO_2 by methanotrophic bacteria as soon as it enters the oxic zone of an aquatic environment. It was found that in the submerged soil without plants, 35 per cent of the produced CH_4 was emitted to the atmosphere (Holzapfel-Pschorn et al., 1986). The presence of rice plants stimulated methanogenesis in the submerged soil but also enhanced the CH_4 oxidation rates within the rhizosphere, so that only about 23 per cent of the produced CH_4 was emitted (Holzapfel-Pschorn et al., 1986). Weed plants in turn did not stimulate methanogenesis but were efficient in supplying oxygen to the rhizosphere so that about 95 per cent of the methane produced underwent oxidation and only 5 per cent was emitted to the atmosphere.

An example of CH_4 emission pattern for an Italian paddy field is shown in Figure 23.2. The emission rates reached about 18 mg

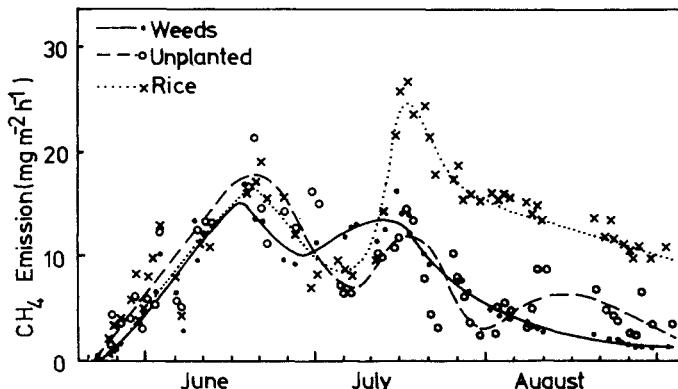
$\text{m}^{-2} \text{ h}^{-1}$ for the unplanted field and for the field covered with weeds, but they reached $26 \text{ mg m}^{-2} \text{ h}^{-1}$ in a rice field. The total amount of methane emitted during the entire vegetation period was 363, 184 and 201 kg ha^{-1} for the rice paddy, the weed and the unplanted field, respectively. Although the presence of rice stimulated emission of methane, the presence of weeds did not (Holzapfel-Pschorn *et al.*, 1986). The emission of methane from Louisiana marshes was between 57 and $2130 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Feijtel *et al.*, 1985).

The emission of methane occurs due to ebullition and/or plant-mediated transport (Dacey and Klug, 1979; Cicerone and Shetter, 1981; Dacey, 1980, 1981; Sebacher *et al.*, 1985; Holzapfel-Pschorn *et al.*, 1986) which may be caused by diffusion related to day-night temperatures (Cicerone and Shetter, 1981) or by pressurised ventilation taking place during the daytime hours (Dacey, 1980, 1981; Dacey and Klug, 1979). The contribution of the plant-mediated transport depends on the kind and developmental stage of the plant cover. It has been found that in an unvegetated paddy field CH_4 was emitted almost exclusively by ebullition, whereas in the presence of well-established plant cover (rice, reed, weeds) 60-94 per cent of CH_4 emission was due to plant-mediated transport (the rice plants being the most efficient in the mediation). Similar figures are given by Dacey and Klug (1979), who found that about 75 per cent of the methane evolved from an eutrophic lake in Michigan escaped through the water plants.

OTHER GASES

Two other gases of importance in flooded soils are N_2 and N_2O because of their role in the processes of nitrogen fixation and denitrification.

Figure 23.2: Methane emission from flooded soils under field conditions in Italy as related to plant cover



Source: Modified from Holzapfel-Pschorn *et al.* (1986)

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Nitrogen fixation reaching 30 kg N ha⁻¹ yr⁻¹ in rice fields is favoured under flooding by providing a photic-oxic water layer and surface soil for phototrophic (free living or symbiotic) blue-green algae and anoxic soil suitable for micro-aerobic and anaerobic heterotrophic bacteria (Wada et al., 1983).

Thus almost all major N₂-fixing groups can grow in this ecosystem and due to this the final N₂ fixation rate depends on many factors. The turnover of nitrogen is complicated by the presence of intensive nitrification occurring in the surface oxidised layer and denitrification below it due to counter diffusion or products of both these processes at the interface between oxidised and reduced soil (Patrick and Reddy, 1976). Thus both these processes contribute to gaseous nitrogen losses in the form of N₂ and N₂O which may be higher than the amount of N₂ fixed.

Nitrous oxide is normally present in atmospheric air at concentrations of 0.3 ppm and interest in it has been stimulated by the concern over the possible destruction of stratospheric ozone by N₂O (Smith et al., 1983). It has been found that reduced soil can act both as a source (at redox potentials above +300 mV) and as a sink of nitrous oxide (at redox potentials below +250mV) (Smith et al., 1983). It seems, however, that flooded soils are normally a source of N₂O (Patrick and Reddy, 1976; Yu Tian-ren, 1980; Yokoyama and Wada, 1984) and their role as sinks is less important because of small concentration gradients likely to occur during N₂O transport from the atmosphere to the soil. The role of plant-mediated transport for N₂O emission has not been fully recognised. Further investigation is necessary to understand to what extent nitrogen transformations in flooded soils are dependent on gas transport processes in order to enable us to manipulate this complicated and multifactoral system.

Another gas related to flooded soils is hydrogen, which reaches 10 per cent of the volume of gases evolving from paddy fields (Patrick and Mikkelsen, 1974). According to Kimura et al. (1984) hydrogen is formed in paddy soils mainly inside the rice roots and is consumed on and/or outside the roots by methanogenic bacteria. The budget of hydrogen in soils and its emission to the atmosphere by ebullition and by plant-mediated transport require further studies.

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Chapter Twenty-four

CHEMISTRY OF METALS AND TRACE ELEMENTS IN A SUBMERGED SOIL*

J.T. Gilmour and P.M. Gale

INTRODUCTION

In reviewing the soil chemical literature regarding metals and trace elements (referred to as metals, hereafter) in submerged soils, one soon finds that iron, manganese, zinc and, to a lesser extent, copper have been most-often studied. Alkaline (sodium, potassium), alkaline earth (calcium, magnesium) and other metals (lead, cadmium, aluminum) have received relatively little attention in the submerged case as compared to unflooded soils.

Several excellent reviews on the chemistry of submerged soils have been published over the years (Ponnamperuma 1972, 1978, 1984; Gambrell and Patrick, 1978; Patrick and Reddy, 1978; Yamane, 1978; Tadano and Yoshida, 1978). We encourage the reader to refer to these reviews and to chapters 21-23 and 25-29 in this book for a more comprehensive view of submerged soils. Our approach will be largely limited to consideration of the solution-solid phase chemistry of the metals with emphasis on studies we have conducted where reasonably complete soil solution data are available.

SOLUTION CONCENTRATIONS VERSUS TIME

When a soil is flooded a sequence of physical and biological phenomena commence which can dramatically influence the chemistry of both the soil solution and solid phases (Ponnamperuma, 1984). Air-filled pores become water filled, and structural units which are not water stable disappear. Infiltration often decreases leading to a reduction in mass flow of solution species across the floodwater-soil interface. As mass flow decreases, diffusion becomes important in the movement of soluble species from the floodwater to the soil solution and vice versa.

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Once the physical properties of the soil are such that the microbial oxygen consumption rate exceeds the oxygen replenishment rate at some soil depth, a submerged soil in the classical sense can develop. Typically, an aerobic zone a few millimeters thick remains at the surface underlain by an anaerobic zone. The chemistry of both the aerobic and anaerobic zones is profoundly influenced by their respective biologies and the suite of chemical reactions commonly found in soils.

The solution metal concentration at a given time is dictated by the kinetics and extent of reactions which increase or decrease metal concentration according to equation (24.1) where M_f is final metal concentration, M_i is initial metal concentration, and the differential, dM/dt , is the difference between reactions which can increase and decrease solution metal concentration.

$$M_f = M_i + dM/dt \quad (24.1)$$

Among the reactions which can alter metal concentrations are: oxidation-reduction; adsorption-desorption; ion exchange; mineral precipitation-dissolution; ion-pair, complex or chelate formation; and the physical movement of metals in response to mass flow and diffusion.

In a sample of field (Yoon, Gilmour and Wells, 1975; Gilmour, 1977; Sonar and Ghugare, 1982; Swarup, 1982; Baker, 1983; Sharma and DeDatta, 1985), greenhouse (IRRI, 1963, 1964; Islam and Islam, 1973; Pasricha and Ponnampерuma, 1976), and laboratory (Olomu, Racz and Cho, 1973; Puttaswamygowda and Pratt, 1973; Rahmatullah, Chandhry and Rashid, 1976; Hess and Blanchard, 1977; Lynch and Gunn, 1978; Mandal and Mitra, 1982; Mahrous, Mikkelsen and Hafaz, 1983; Sims and Patrick, 1978) studies, four types of concentration versus time data emerged for iron, manganese, copper and zinc. Figure 24.1 illustrates these concentration-time curves, whereas Table 24.1 presents the frequency of occurrence of the curve types among the metals iron, manganese, copper and zinc.

Type I curves typified a majority of iron and manganese data and were characterised by a rapid increase in concentration followed by a slower decrease to relatively stable values. The rapid increase in iron and manganese was largely attributed to soil reduction (Islam and Islam, 1973; Patrick and Henderson, 1980) and formation of chelates with fermentation products which appear soon after submergence (Gotoh and Patrick, 1972; Tadano and Yoshida, 1978; Tian-Ren, 1983). The peak concentrations of iron and manganese have been related to soil properties such as aerobic pH and soil organic matter content (IRRI, 1963, 1964; Mahrous et al., 1983). Figure 24.2 illustrates these relationships for our data set excluding the low temperature data of Olomu et al., (1973). The decrease which followed the peak concentration was considered to be the result of decreased chelation (Reddy and Patrick, 1977), solid phase formation (Ponnampерuma, Loy and Tiano, 1969; Schwab and Lindsay, 1983), and/or adsorption by surfaces created under anaerobic conditions (Collins and Buol, 1970; Gambrell and Patrick, 1978; Iu, Pulford and Duncan, 1981a). A variant of the Type I curve, the Type II curve, was common where conditions

Figure 24.1: Curve types for solution metal concentrations versus time in flooded soils

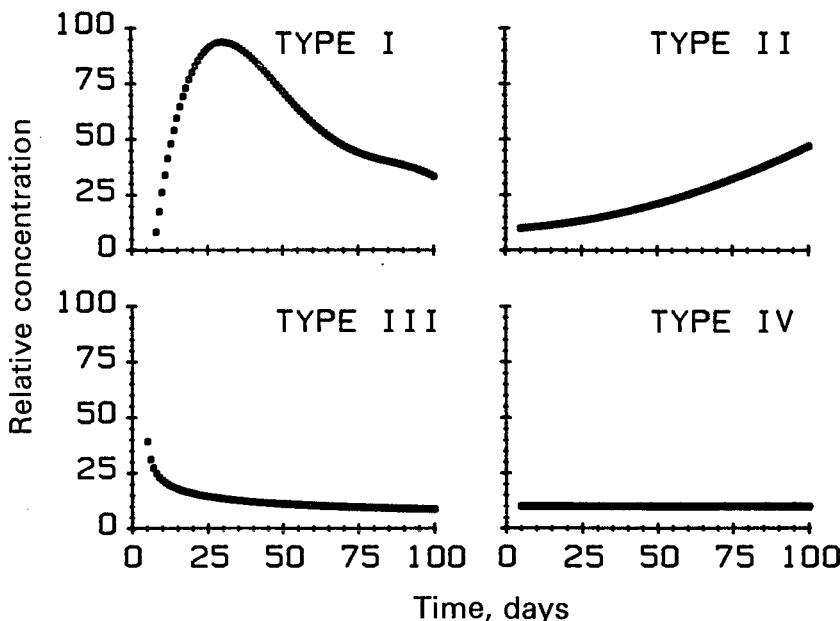


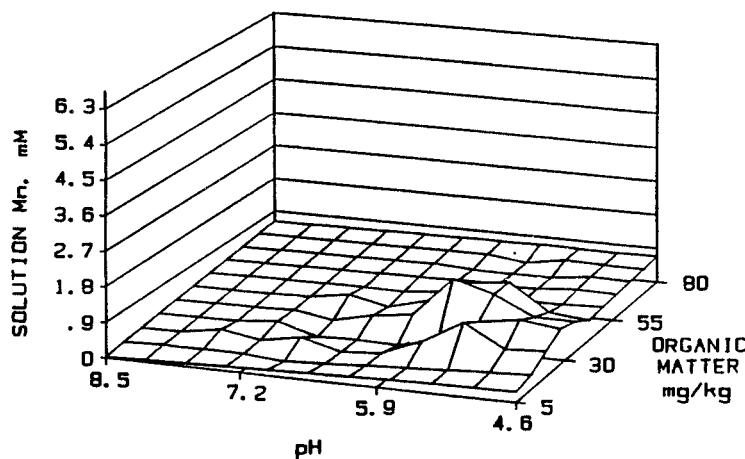
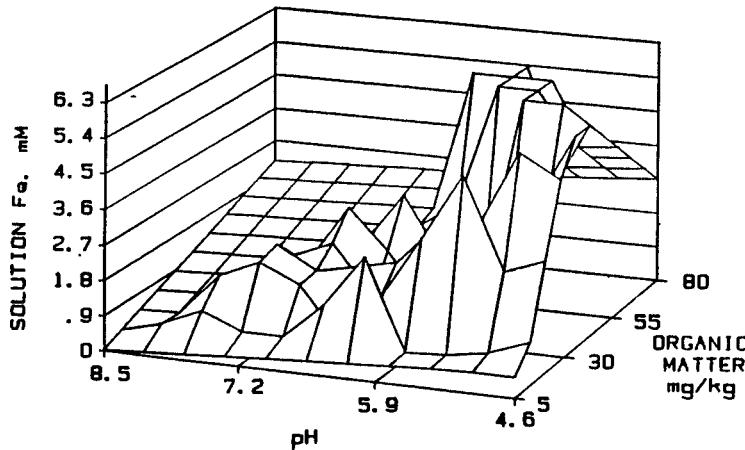
Table 24.1: Frequency of occurrence (%) of curve types among the four most studied metals

Metal	Observations	Curve type %			
		I	II	III	IV
Iron	63	56	27	0	17
Manganese	63	62	19	0	19
Copper	6	0	0	16	83
Zinc	16	19	0	50	31

such as low temperature (Lynch and Gunn, 1978; Ponnamperuma, 1984) and lack of oxidizable organic substrates (Sonar and Ghugare, 1982; Swarup, 1982) limited the rate and/or extent of reduction and, thus, extended the time to peak solution concentrations. The Type II scenario was represented by 27 and 19 per cent of the iron and manganese data, respectively.

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Figure 24.2: Type I curve peak concentrations for iron and manganese as a function of initial soil pH and soil organic matter



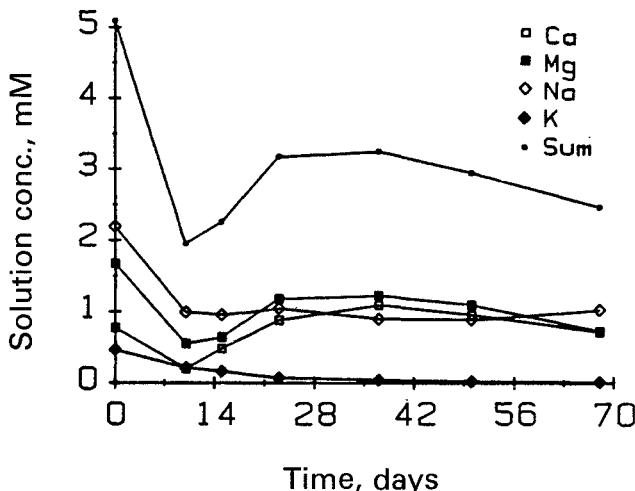
In the Type III case there was a rapid decrease in concentration to relatively stable values, while Type IV curves showed relatively stable values throughout time. It is possible the Type IV cases are a variant of the Type III case where initial, higher concentrations were not reported due to lack of samples at flooding. All the copper data and 81 per cent of the zinc data followed Type III or Type IV patterns which suggested that equilibrium conditions between the solution and solid phases were established soon after submergence by mechanisms which could include mineral

precipitation-dissolution and/or adsorption-desorption phenomena (Mandal and Haldar, 1980; Iu et al., 1981b; Bjerra and Schierup, 1985). The rapid decline noted initially in the Type III case was difficult to assess, but could be due to precipitation, adsorption, and/or entry of floodwater which could both dilute and transport metals. Apparently, chelation which should coincide with peak soluble carbon concentrations two to four weeks after flooding does not override the latter reactions (Reddy and Patrick, 1977; Sommers and Lindsay, 1979).

The sum of the alkaline and alkaline-earth metal concentrations has been found to follow the Type I curve (Ponnampерuma, 1972). In a Crowley silt loam (Typic Albaqualfs) cropped to rice (*Oryza sativa* L.), Yoon (unpublished data, 1973) found an initial depression in the sum of the metals followed by a Type I relationship as presented in Figure 24.3. The initial decrease was assumed to be due to dilution of the soil water by infiltration of floodwater from a reservoir fed by surface water. While cation exchange undoubtedly influenced the data in Figure 24.3, no precipitation of divalent carbonates was found as the soil solutions were undersaturated by one to three orders of magnitude in regard to both calcite and magnesite. The divalent cation peaks coincided with the increase in manganous and ferrous species which could participate in cation-exchange reactions and with the probable increase in fermentation products with chelation properties in the solution (Puttaswamygowda and Pratt, 1973; Lynch and Gunn, 1978).

The decreases in calcium and magnesium concentrations coincided with small decreases in ferrous and manganous concentrations and a probable decrease in organic chelates (Meek,

Figure 24.3: Time dependency of alkaline and alkaline-earth metal concentrations in a flooded Crowley silt loam



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Mackenzie and Grass, 1968; Lynch and Gunn, 1978). Sodium and potassium followed Type III relationships and did not appear to be substantially influenced by chelation or cation exchange phenomena. The systematic depression in potassium was attributed to plant uptake.

EQUILIBRIUM CHEMISTRY

In order to assess the behaviour of metals in flooded soils from an equilibrium standpoint, it was necessary to have rather complete solution chemistry for soils which had been flooded for an extended period of time in order to minimise the influences of flood-water infiltration, reaction kinetics, and organic chelates. In Arkansas, such data were available for five fields of the Crowley silt loam which had been flooded for more than 70 days (Gilmour and Kittrick, 1979) and five fields of the Sharkey clay or silty clay (Vertic Haplaquepts) which had been flooded for more than 80 days (Baker, 1983) and cropped to rice. Soil solutions were obtained from a 0-10 cm mud sample and analysed using the methods described by Gilmour and Kittrick (1979). The ranges and mean total concentrations for the soil solution data are given in Table 24.2.

The computer program GEOCHEM (Sposito and Mattigod, 1979) was used to compute solution ion, ion-pair and complex concentrations. Table 24.3 presents a summary of these data. Little ion-pair or complex formation was found for calcium, magnesium, sodium, and potassium. The bicarbonate and carbonate ion-pairs were important for iron, manganese, zinc, and copper where free metal percentages were 22, 60, 28, and <1 per cent of total metal concentrations, respectively. Hydrolysis of aluminium left less than one per cent of the total aluminium in the uncomplexed form. It should be emphasized that the ion-pair and complex calculations were made using stability constants resident in GEOCHEM which may differ from those found in other sources. An example of this is the aluminium case where GEOCHEM predicts Al(OH)_4^- to predominate and Lindsay (1979) predicts Al(OH)_3 to predominate at the pH of the Sharkey soil.

Free concentrations of the metals and ligands were used to compute the negative logarithms of the ion activity products (pIAP) for solid phases which might form. Activity corrections were made using the Davies Equation (Sposito, 1984). These pIAP values were then compared to published solubility products (pK) from Lindsay (1979) and Stumm and Morgan (1981). Table 24.4 presents the results of these calculations for all solids which were either supersaturated or within one order of magnitude of saturation. Supersaturation was defined as $\text{pIAP} < \text{pK}$. When $\text{pIAP} = \text{pK}$, formation of the solid phase in question is possible and, perhaps, probable. Where supersaturation was found, a kinetic limitation to solid phase formation, or a shift in the activity of the solid phase from unity (unit activity of the solid phase was assumed in the following computations) precludes interpretation. The reader is referred to Sposito (1981) and Stumm and Morgan (1981) for a discussion of these effects.

Table 24.2: Ranges and mean total metal concentrations in flooded Sharkey and Crowley soils

Species	Units	Crowley range	Crowley mean	Sharkey range	Sharkey mean
Ca	M x 10 ³	1.0 - 3.2	2.2	2.6 - 4.4	3.7
Mg	M x 10 ³	0.3 - 1.6	1.2	1.7 - 2.7	2.2
K	M x 10 ⁴	1.0 - 3.0	2.0	0.5 - 1.7	1.1
Na	M x 10 ³	1.7 - 3.3	2.5	0.3 - 0.5	0.4
Fe	M x 10 ⁴	2.0 - 6.0	3.4	2.6 - 4.5	3.5
Mn	M x 10 ⁴	2.0 - 12.6	5.9	1.9 - 5.5	3.1
Zn	M x 10 ⁶	5.0 - 7.6	6.6	-	-
Cu	M x 10 ⁶	-	-	1.6 - 4.8	3.5
Al	M x 10 ⁵	-	-	1.1 - 2.2	1.8
HCO ₃	M x 10 ³	5.6 - 13.8	9.8	9.6 - 15.1	12.8
SO ₄	M x 10 ⁵	0.05 - 0.4	0.1	4.3 - 23.4	8.4
Cl	M x 10 ⁴	6.0 - 18.2	11.0	0.1 - 5.5	2.5
S	M x 10 ^{1a}	5.9 - 6.3	6.2	6.3 - 9.8	8.6
PO ₄ -P	M x 10 ⁵	0.3 - 2.0	0.9	0.3 - 4.6	1.9
H ₄ SiO ₄	M x 10 ⁴	2.3 - 6.5	3.8	1.0 - 1.6	1.3
I	M x 10 ²	1.0 - 1.8	1.3	1.2 - 1.9	1.7
pH	-	6.8 - 7.3	7.1	7.0 - 7.5	7.3

Note: a, assumes pH₂S = 10.3

The pIAP values for the carbonates calcite, aragonite, siderite, and rhodocrosite were close to published pK values which suggested that these solids could be present and influence solution concentrations of calcium, iron, and manganese, respectively. The results for the calcium carbonates were likely due to irrigation with well water known to be supersaturated with respect to calcite and aragonite (Gilmour, Shirk, Ferguson and Griffis, 1977). The calcium carbonate solubility products were near the value of 7.95 reported by Suarez (1977) for well waters. The supersaturation with respect to siderite and rhodocrosite agreed with Ponnamperuma (1984) who stated that siderite was a possible solid phase and that manganese carbonate was the sole solid phase influencing solution manganese concentrations. The zinc and copper carbonates, smithsonite and malachite, were undersaturated by about one order of magnitude. Azurite, Cu₃(OH)₂(CO₃)₂, was only slightly more undersaturated than malachite, whereas CuCO₃ was undersaturated by nearly four orders of magnitude.

The pIAPs of the metal sulfides listed by Lindsay (1979) indicated supersaturation. The zinc sulfide, sphalerite, was slightly supersaturated as reported previously by Gilmour and Kittrick (1979). A small shift in pH₂S or chelation by soluble organics would cause exact agreement between pK and pIAP, thus, sphalerite appears to influence solution zinc concentrations. Large

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Table 24.3: Solution ion, ion-pair and complex ion percentages computed using GEOCHEM for data shown in Table 24.2

Species	Crowley		Sharkey	
	range	mean % of total	range	mean
Ca^{2+}	92 - 97	94	92 - 94	93
CaHCO_3^+	3 - 7	5	5 - 7	6
Mg^{2+}	94 - 97	95	94 - 95	94
MgHCO_3^+	2 - 6	4	4 - 5	5
K^+	-	>99	-	>99
Na^+	-	>99	-	99
NaHCO_3^+	-	-	-	1
Fe^{2+}	20 - 45	29	20 - 23	22
FeHCO_3^+	48 - 62	56	47 - 64	55
FeCO_3°	6 - 20	15	13 - 27	23
Mn^{2+}	57 - 80	66	56 - 61	60
MnHCO_3^+	17 - 35	27	26 - 35	30
MnCO_3°	2 - 8	6	5 - 13	10
Zn^{2+}	20 - 42	28	-	-
ZnHCO_3^+	56 - 74	67	-	-
ZnCO_3°	2 - 6	5	-	-
Cu^{2+}	-	-	-	<1
CuHCO_3^+	-	-	72 - 87	77
CuCO_3°	-	-	11 - 29	21
Al^{3+}	-	-	-	<1
Al(OH)_4^-	-	-	52 - 77	67
Al(OH)_3°	-	-	23 - 48	33

supersaturation was found for the iron (pyrite) and copper (covellite) cases. The iron sulfide, troilite, which Ponnamperuma (1984) suggested could form in flooded soils was undersaturated by about five orders of magnitude. Undersaturation of the sulfides of calcium, magnesium, and manganese also was observed for both soils.

Large supersaturation was calculated for the oxide (magnetite) and hydroxide ($\text{Fe}_3(\text{OH})_8$) of ferrous iron with the oxide being more supersaturated than the hydroxide. Ponnamperuma (1984) and Schwab and Lindsay (1983) listed magnetite as a possible solid phase of iron. Aluminium concentrations appeared to be controlled

by amorphous aluminium hydroxide as the pIAP value for the Sharkey soil was intermediate to reported pK values. The pIAP for Al(OH)_3 was within the range of values commonly found in soils (Hsu, 1977). The pIAPs for hydroxides of the other metals were much larger than their respective pKs and, thus, would not be expected to form.

Formation of a number of phosphates appeared possible. Slight undersaturation with respect to beta-calcium phosphate, vivianite (depending on choice of pK), and variscite was found. Vivianite (Nriagu, 1972) and beta-calcium phosphate (Norvell, 1974) have been reported to form in sediments and variscite was found to be the stable form of phosphate in acid soils (Lindsay and Vlek, 1977). Large supersaturation for hydroxyapatite and manganese phosphate was observed. The presence of the iron phosphate, strengite, was tested using ferric iron solubility data of Lindsay (1979). Both soils were undersaturated with respect to strengite by about three orders of magnitude.

The pIAPs for metal silicates were evaluated and all calculations showed at least three orders of magnitude undersaturation. The range in silicic acid concentrations was within that common for soils (Lindsay, 1979). Thus, formation of metal silicates was not likely in either the Crowley or Sharkey soils.

CONCLUSIONS

The dynamic nature of the solution metal concentrations with time can be characterised by four types of concentration versus time relationships. Changes in solution metal concentration represent the result of reactions which increase metal concentration in solution and those which decrease concentration. Type I was characteristic for Fe and Mn where a rapid increase in concentration was followed by a slower decrease. Type II was a variant of Type I where the initial peak was not reached and a slow increase in metal concentration was observed over time. Iron and Mn followed this pattern when conditions were not conducive for rapid soil reduction. Type III characterized by a rapid decline in initial concentrations to stable values and Type IV where stable values were observed throughout time were typical for Zn and Cu. The sum of the alkaline and alkaline-earth cations tended to follow the Type I pattern with Ca and Mg predominating.

After sufficient time, the variations in solution metal concentrations with time becomes smaller and potential for equilibrium between solution and solid phases increases. Data from Crowley silt loam and Sharkey clay or silty clay cropped to rice and flooded for more than 70 days were used to evaluate equilibrium chemistry. Free solution concentrations of Fe, Mn, Cu and Zn were altered by formation of bicarbonate-carbonate ion-pairs, while free Al concentrations were altered by hydrolysis reactions. The impact of ion-pairs on Ca, Mg, Na and K was small. Solid phases most likely forming and affecting metal concentrations were calcite-aragonite, rhodocrosite, siderite, sphalerite, amorphous Al(OH)_3 , vivianite, and variscite. Large supersaturation was found for pyrite, covellite, magnetite, $\text{Fe}_3(\text{OH})_8$, hydroxyapatite and MnPO_4 .

Table 24.4: Solid phases near saturation or supersaturated in flooded Sharkey and Crowley soils

Reaction	I ^a	pK	II ^b	Crowley	Mean pIAP Sharkey
Carbonates					
CaCO_3 (calcite) = $\text{Ca}^{2+} + \text{CO}_3^{2-}$	8.41	8.42	8.3	7.7	7.7
CaCO_3 (aragonite) = $\text{Ca}^{2+} + \text{CO}_3^{2-}$	8.18	8.22	8.3	7.7	7.7
MgCO_3 (magnesite) = $\text{Mg}^{2+} + \text{CO}_3^{2-}$	7.46	7.46	7.9	8.0	
FeCO_3 (siderite) = $\text{Fe}^{2+} + \text{CO}_3^{2-}$	10.23	10.7	9.6	9.4	
MnCO_3 (rhodocrosite) = $\text{Mn}^{2+} + \text{CO}_3^{2-}$	10.07	10.4	9.1	9.0	
ZnCO_3 (smithsonite) = $\text{Zn}^{2+} + \text{CO}_3^{2-}$	10.24	10.20	11.3	—	
$\text{Cu}_2(\text{OH})_2\text{CO}_3$ (malachite) = $2\text{Cu}^{2+} + 2\text{OH}^- + \text{CO}_3^{2-}$	33.16	—	—	33.9	
Sulfides					
FeS_2 (pyrite) + $2\text{e}^- = \text{Fe}^{2+} + 2\text{S}^{2-}$	42.52	—	34.7 ^c	34.0 ^c	
$\alpha\text{-ZnS}$ (sphalerite) = $\text{Zn}^{2+} + \text{S}^{2-}$	24.70	—	23.2	—	
CuS (covellite) = $\text{Cu}^{2+} + \text{S}^{2-}$	36.10	—	—	24.8	
Fe_3O_4 (magnetite) + $8\text{H}^+ + 2\text{e}^- = 3\text{Fe}^{2+} + 4\text{H}_2\text{O}$	—35.69	—	-46.2 ^c	-47.6 ^c	

Table 24.4 (continued)

		Hydroxides			
$\text{Fe}_3(\text{OH})_8(s) + 8\text{H}^+ + 2e^- = \text{Fe}^{2+} + 8\text{H}_2\text{O}$		-43.75	-	-48.4	-49.8
$\text{Al(OH)}_3 \text{ (amorphous)} = \text{Al}^{3+} + 3\text{OH}^-$		32.45	31.2	-	32.3
$\text{Ca}_5(\text{PO}_4)_3\text{OH} \text{ (hydroxyapatite)} = 5\text{Ca}^{2+} + 3\text{PO}_4^{3-} + \text{OH}^-$	Phosphates	58.19	57	54.8	51.9
$\beta\text{-Ca}_3(\text{PO}_4)_2 = 3\text{Ca}^{2+} + 2\text{PO}_4^{3-}$		28.92	-	31.0	29.3
$\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O} \text{ (vivianite)} = 3\text{Fe}^{2+} + 2\text{PO}_4^{3-} + 8\text{H}_2\text{O}$		35.9	32	34.9	34.1
$\text{MnHPO}_4(s) = \text{Mn}^{2+} + \text{PO}_4^{3-} + \text{H}^+$		25.29	-	21.9	21.9
$\text{AlPO}_4 \cdot 2\text{H}_2\text{O} \text{ (variscite)} = \text{Al}^{3+} + \text{PO}_4^{3-} + 2\text{H}_2\text{O}$		22.05	21	-	22.6

Notes: a, from Lindsay (1979); b, from Stumm and Morgan (1981); c, assumes $\text{pe}^- = 2$ ($\text{Eh}=120$ mv).

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Chapter Twenty-five

PHOSPHORUS TRANSFORMATIONS IN FLOODED SOILS

L.R. Hossner and W.H. Baker

INTRODUCTION

Flooding a soil changes the availability of many plant nutrients. This is principally due to oxidation-reduction processes as a result of the restriction of oxygen movement to the soil by the overlying water. Consequently, the behaviour of phosphorus under flooded conditions is found to be quite different from that under upland conditions. The importance of understanding the behaviour of phosphorus under flooded conditions can be seen from estimates which indicate that 40 per cent of the world's population relies on rice as a major source of calories. Man has benefited greatly from the application of phosphorus fertilizers to agronomic crops. Indeed, phosphorus deficiency in plants is second only to nitrogen deficiency as the major soil fertility problem throughout the world. Recent environmental restrictions and economic trends have dictated that only that quantity of fertilizer nutrients which will support an economic return be applied in order to allow producers to be more competitive in world markets. This chapter deals with the transformations of inorganic phosphorus after a soil is flooded, its various forms in flooded soils, and its transformation after a flooded soil is drained.

PHOSPHORUS AVAILABILITY AFTER A SOIL IS FLOODED

One of the most striking features of phosphorus chemistry in flooded soils is the increase in soil solution phosphate concentration soon after applying the flood. For soils where a large amount of phosphorus has not been applied, the soil solution phosphate concentration is found to increase rapidly followed by a gradual decrease to some equilibrium value characteristic of the soil (Figure 25.1) (Ponnamperuma, 1972). In soils which have received significant applications of phosphorus, the phosphate level after submergence is found to decrease with time from an initial high concentration to a much lower level depending on the soil and the amount of phosphorus applied (Hossner, Freeouf and Folsom, 1973). Soils that require the addition of phosphorus fertilizer in order to produce adequate yields of upland crops will, when flooded, often supply enough phosphorus from native sources to

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meet the phosphorus requirements of flooded crops such as rice, where an average solution phosphorus concentration of 0.1 ppm has been shown to be sufficient to obtain 90 per cent of maximum yield in most instances (Figure 25.2) (Hossner et al., 1973). However, the availability of added phosphorus to plants under flooded conditions is not easily predicted.

Various mechanisms have been suggested to explain the effect of anaerobic conditions on the change in phosphorus solubility. One factor, which is a direct result of application of the flood, is an increase of the diffusion of phosphorus (Mahtab, Godfrey, Swoboda and Thomas, 1971). Because diffusion is a major process by which phosphorus moves in soils, Turner and Gilliam (1976) have proposed that the increase in phosphorus availability upon flooding a soil is largely a result of an enhancement of the phosphorus diffusion coefficient (Figure 25.3).

After a flooded soil becomes deficient in oxygen, oxidized forms of manganese and iron eventually become the major electron acceptors for the facultative and anaerobic microbes. The reduction of manganese and iron is evident due to the increased solution concentration of their soluble divalent forms after flooding (Figure 25.4) (Patrick and Delaune, 1972; Gotoh and Patrick, 1972, 1974; Schwab and Lindsay, 1983a,b). Thus, one of the proposed mechanisms for the observed release of phosphorus from soils upon submergence is the reductive dissolution of Fe(III) and Mn(IV) phosphate minerals (Patrick, 1964; Patrick, Gotoh and Williams, 1973; Willett, 1985).

Figure 25.1: Water soluble phosphorus as a function of time after flooding (from Ponnamperuma, 1972)

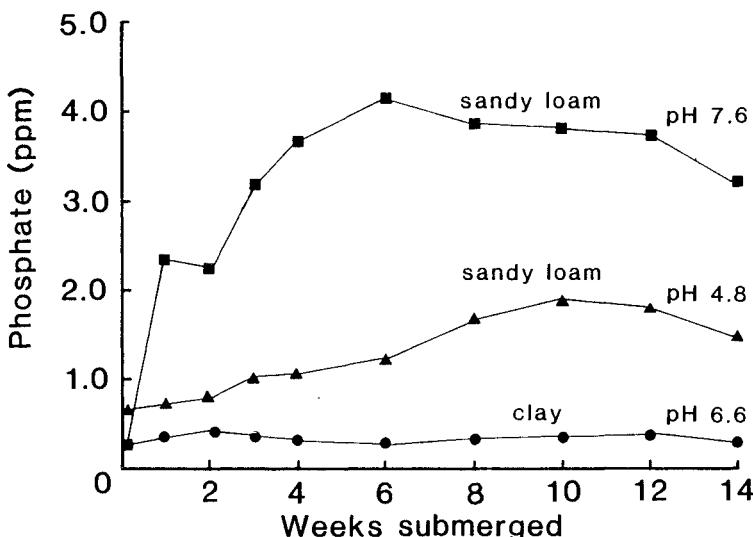


Figure 25.2: Relative yield of rice as influenced by the average soil solution phosphorus concentration (from Hossner et al., 1973)

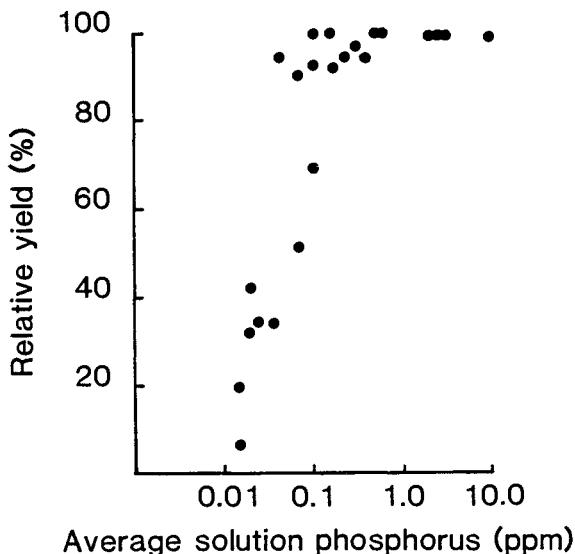
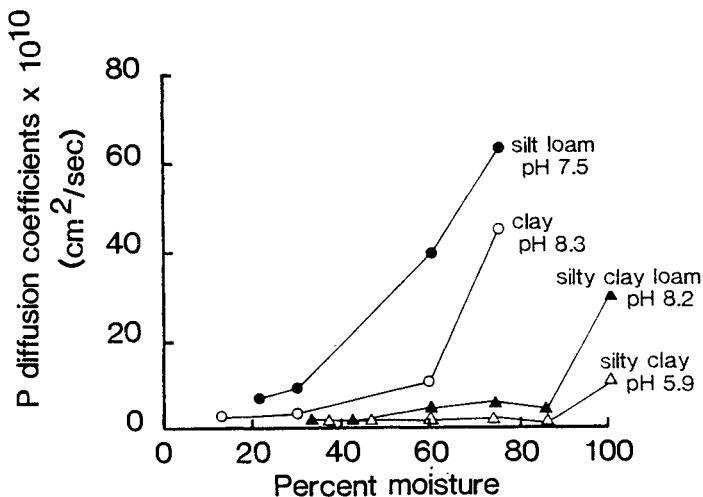
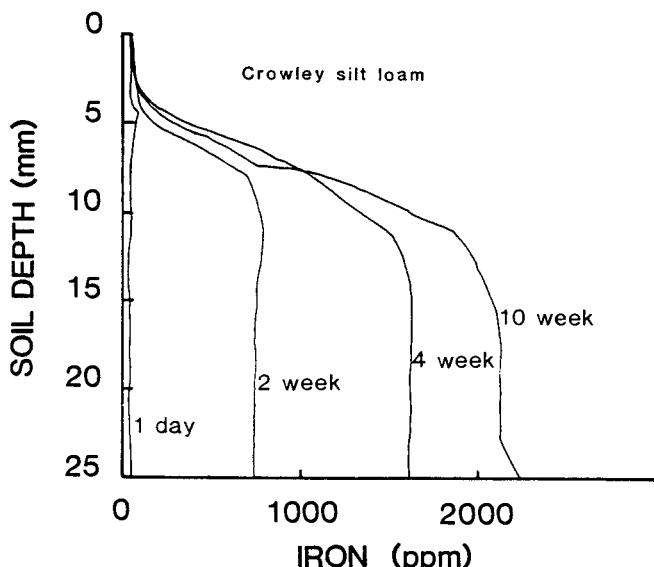


Figure 25.3: Effect of moisture on the diffusivity factor. The final point on each curve represents D-values at water saturation (from Turner and Gilliam, 1976)



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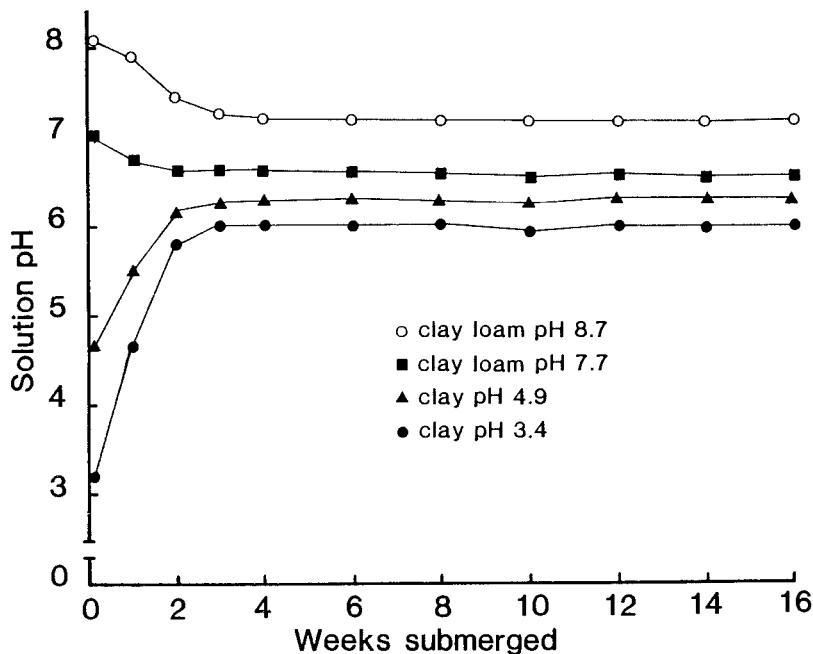
Figure 25.4: Vertical distribution of Fe(II) at various times after flooding (from Patrick and DeLaune, 1972)



A few weeks after submergence, the pH of most acid and alkaline soils converge to pH values near 7 (Figure 25.5). Variations of solution pH values of this magnitude are sufficient to change the solubility of some minerals even though these pH changes do not represent as great a potential difference as those associated with changes in the redox potential after flooding. Among the more likely compounds involved in buffering the pH of waterlogged soils are the iron and manganese compounds discussed above, and the chemical equilibria that exist between the carbonic acid and aquatic organism CO₂ metabolism (Ponnampерuma, Castro and Valencia, 1969; Mikkelsen, De Datta and Obcemea, 1978). Soon after submergence the accumulation of CO₂ will depress the pH for alkaline soils, while the increase in pH of acid soils is due to the ensuing reduction reactions which involve the consumption of hydrogen ions (Ponnampерuma; 1972). In situations where the flooded soil is initially acidic, the effect of increasing pH brought about by soil reduction can result in the hydrolysis of iron and aluminum phosphates. However, in alkaline soils, the decrease in the soil pH because of the higher CO₂ partial pressure can result in the dissolution of calcium phosphate minerals.

Although a submerged soil or sediment experiences a low rate of gas exchange, oxygen is not entirely absent. In many instances a submerged soil is differentiated into two distinct aerobic and anaerobic zones (Pearsall and Mortimer, 1939; Mortimer 1941, 1942;

Figure 25.5: Effect of flooding on the solution pH (from Ponnamperuma, 1972)



de Gee, 1950). The oxygen concentration at the soil-water interface may be high in a soil surface layer extending down to several millimeters. Below this oxidized layer, only reduced constituents are found due to the limited diffusion of oxygen. The development and thickness of the oxidized surface layer is determined by the diffusion rate of oxygen at the soil-water interface and the consumption of oxygen by microbial respiration and chemical oxidation of the mud (Howeler and Bouldin, 1971; Patrick and Delaune, 1972). However, De Datta (1981) also adds that, in many flooded soils, there may be small oxidized pockets in the reduced soil matrix and oxidized streaks corresponding to root channels. A good example of this in rice soils is the precipitation of iron and manganese oxides on the roots of rice due to the ability of the rice plant to translocate oxygen down to its root system from its aerial parts (Howeler, 1973; Bacha and Hossner, 1977). Thus, in flooded soil systems supporting aquatic plants such as rice, the distinction between reduced and oxidized phosphate constituents may not be entirely clear.

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PHOSPHORUS REACTION PRODUCTS IN SEDIMENTS AND SUBMERGED SOILS

Most of the discrete solid phase phosphorus compounds in soils are of low total content in the clay fraction, and therefore are difficult to characterize. A large amount of the phosphorus in soil and sediments is present in the organic fraction. This complicates the system due to the dynamic equilibria between organic and inorganic phosphorus forms (Sommers, Harris, Williams, Armstrong and Syers, 1972). In spite of these difficulties, various direct methods have been used successfully to determine discrete phosphate mineral phases in flooded soils and sediments. In general, solid phase phosphate compounds are believed to exist as various insoluble compounds such as strengite, $\text{FePO}_4 \cdot 2\text{H}_2\text{O}$, vivianite, $\text{Fe}_3(\text{PO}_4)_2 \cdot 8\text{H}_2\text{O}$, variscite, $\text{AlPO}_4 \cdot 2\text{H}_2\text{O}$, or hydroxyapatite, $\text{Ca}_5(\text{PO}_4)_3\text{OH}$ (Syers, Harris and Armstrong, 1973; Lindsay, 1979).

Using a petrographic microscope, Dell (1973) and Nriagu and Dell (1974) identified vivianite nodules (averaging about 60 μm) ranging from crystalline to poorly crystalline forms in sediments of the Great Lakes. Sawhney (1973) found discrete phosphate grains in lake sediments to exist as complex compounds containing variable amounts of aluminium, iron, silica, calcium, and phosphorus based on electron microprobe analysis. He noted that none of the samples examined corresponded to strengite or variscite, although a few samples did appear to be similar to apatite. Cescas, Tyner and Syers (1970), using this same method, identified apatite minerals in weathered ash and sediments. However, Qureshi and Jenkins (1978) found phosphorus to be uniformly distributed within calcite grains of a marine clay soil, as opposed to being concentrated as discrete calcium phosphates.

Because of the difficulty in identifying phosphorus reaction products in soils, many investigations have employed solubility product measurements as a means of indirectly determining possible phosphate solid phases. There are certain problems stemming from the need for estimating reliable activity coefficients for all species and dissociation constants for the complex species which are encountered with solubility product determinations (Adams, 1971; Nakayama, 1971). Several computer programs are available such as GEOCHEM (Sposito and Mattigod, 1979) and WATEQ2-A (Bail, Jenne and Nordstrom, 1980) which can provide the user with a fairly comprehensive chemical speciation of the major free ions in solutions (Baham, 1984). However, sediments generally contain assemblages of minerals quite different from those which would be predicted from equilibrium thermodynamics. This can mainly be attributed to the dynamic nature of natural systems which tends to preclude the use of equilibrium thermodynamics as a good frame of reference.

Lindsay (1979) and Lindsay and Vlek (1977) have constructed phase diagrams which illustrate the effect of redox on the solubility of iron and aluminium phosphates. For an acid soil in which aluminium is controlled by kaolinite-quartz and Fe(III) is controlled by soil-Fe, these isotherms show that vivianite would be the stable phosphate phase below a $\text{pH} + \text{pH}$ value of 7.92, with strengite controlling the solution phosphate level above this value (Lindsay

and Vlek, 1977). In the case of a more highly weathered soil where goethite is controlling Fe(III) activity and gibbsite is controlling the solution aluminum activity, variscite would be predicted to be the stable phosphate mineral phase (Lindsay, 1979).

The solubility of calcium phosphates decrease in the order octacalcium phosphate, $\text{Ca}_4\text{H}(\text{PO}_4)_3 \cdot 2.5\text{H}_2\text{O}$, tricalcium phosphate, $\beta\text{-Ca}_3(\text{PO}_4)_2$, and hydroxyapatite. While activity products for crystalline hydroxyapatite in the absence of fluorine have been observed in flooded alkaline soils and sediments, there is often some kinetic limitation which precedes the formation of apatite resulting in supersaturation with respect to its solid phase solubility product (Nancollas, Amjad and Koutsoukos, 1979).

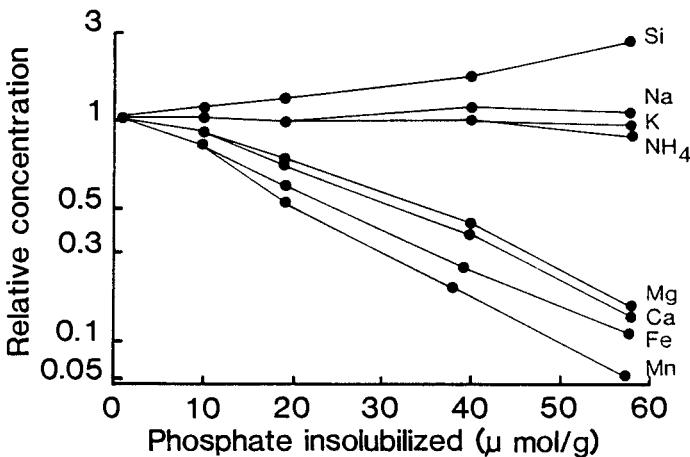
Nriagu (1972) and Nriagu and Dell (1974) used solubility data to show vivianite to be the stable and most probable phosphate mineral in reduced lake sediments. They concluded that the precipitation and dissolution of vivianite in lake sediments served as an important buffer mechanism by which the levels of phosphorus were regulated in the interstitial waters. Norvell (1974) monitored the loss of solution phosphate in lake sediments under oxygen-free conditions and suggested that calcium, iron, and manganese phosphate compounds are effective in limiting the solubility of inorganic phosphate in anoxic lake sediments (Figure 25.6). The best agreement between observed and crystalline activity products was for tricalcium phosphate both before and after additions of phosphate to these sediments. Norvell (1974) concluded that phosphate compounds were precipitated as intergrades or partially substituted Fe/Mn amorphous hydroxyapatite or tricalcium phosphate. Results from a study by Holford and Patrick (1979) suggested that soil suspensions reduced to a redox potential of -150 mV at pH 5 were precipitating vivianite at high phosphate levels. At a pH of 8 and a Eh of -150 mV, phosphate removal from solution at higher added phosphate concentrations was suggested to be due to the precipitation of calcium phosphate compounds.

The retention of phosphorus by sediments and flooded soils has also been attributed to an adsorption mechanism. However, the distinction between adsorption and precipitation is difficult to resolve. Several workers have suggested that adsorption and precipitation in soils are part of the same process, where the slower reaction following a rapid initial sorption reaction is assumed to be due to precipitation (Kittrick and Jackson, 1956; Hsu, 1964; Bache, 1964; van Riemsdijk and de Haan, 1981). Perhaps the best illustration of this concept is given by Griffin and Jurinak (1973) where data for the sorption of phosphate by calcite were separated into two distinct regions when plotted as a Langmuir isotherm. They interpreted this two-region isotherm as resulting from an initial sorption of phosphate on a limited number of surface sites, followed by the formation of surface clusters of phosphate ions and eventual nucleation from which calcium phosphate crystal growth could occur.

The role of amorphous iron and aluminium hydrous oxides in the adsorption of phosphorus by reduced sediments and soils has been discussed by Shukla, Syers, Williams, Armstrong and Harris (1971), Li, Armstrong, Williams, Harris and Syers (1972), and Khalid, Patrick and DeLaune (1977). It has been postulated that a

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Figure 25.6: Influence of added phosphate on the solubility of several interstitial solution species. The concentration of each species is expressed as a fraction of its concentration in the control sediment (from Norvell, 1974)



gel complex of hydrated iron oxide, possibly in conjunction with aluminium hydroxide and smaller amounts of silica hydroxide and organic matter, is the major phosphorus sorbing component of flooded soils and sediments based on aluminium and iron-fractionation schemes (Mahapatra and Patrick, 1969; Williams, Syers, Harris and Armstrong, 1971) and a close correlation between the amount of oxalate-extractable iron to the amount of phosphate removed from solution (Figures 25.7 and 25.8) (Shukla et al., 1971; Khalid et al., 1977). The structure of the ion-surface bond for the specific adsorption of phosphorus by iron has been shown from infrared analysis by Parfitt, Atkinson and Smart (1975) to occur as a binuclear type of complex. This structure is similar to that proposed earlier by Kafkafi, Posner and Quirk (1967) and by Hingston, Atkinson, Posner and Quirk (1967) for aluminium. These observations suggest that, depending on pH, the principal mechanism of orthophosphate adsorption in non-calcareous soils involves ligand exchange with water, hydroxyl groups, and less specifically adsorbed ligands such as silicate, sulfate, and nitrate (Harrison and Berkheiser, 1982). An excellent review by Parfitt (1978) provides a more detailed discussion on this subject.

REACTION PRODUCTS AND PHOSPHORUS AVAILABILITY WHEN A SUBMERGED SOIL IS DRAINED

When a flooded soil is drained, many of the phosphorus minerals are altered to mineral forms which are stable under oxidized con-

Figure 25.7: Effect of flooding on transformation of inorganic phosphate (from Patrick and Mahapatra, 1968)

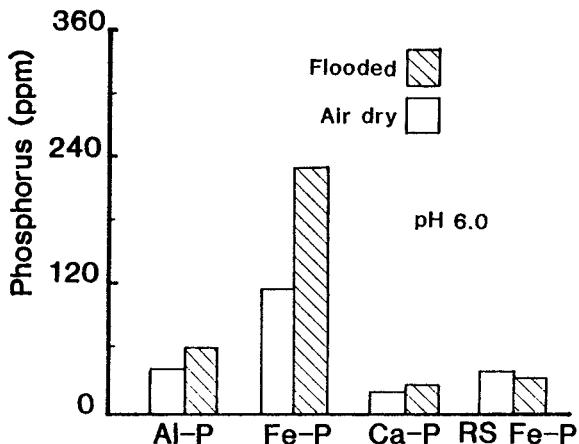
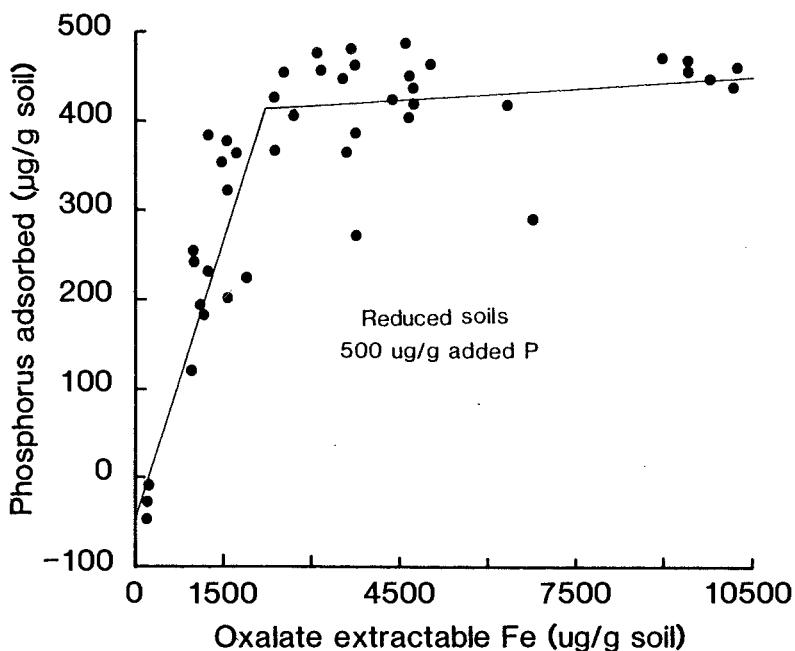


Figure 25.8: Relationship between oxalate extractable Fe and phosphorus sorbed under reduced conditions (from Kahlid et al., 1977)



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ditions. In many instances, upland crops grown in rotation with flooded rice, or on soils which have been anaerobic for a short time, frequently show poor growth and acute phosphorus deficiency symptoms (Petersen, Salsbery and Martin, 1972; Brandon and Mikkelsen, 1979). Thus, phosphorus may go from a soluble and available form during submergence, to a much more insoluble and unavailable form when the soil is drained.

Because the reoxidation process is fairly rapid, crystalline minerals may not form initially. Instead, it has been suggested that phosphorus may be retained by the soil on the surfaces of amorphous iron gel-like compounds in some type of chemisorbed form (Shukla et al., 1971; Sah and Mikkelsen, 1986). Characterizing the availability of these initial phosphate precipitates is very complex due to their amorphous nature where they may show solubilities that are 10 to 100 times greater than the crystalline minerals (Lindsay, 1979). In time, phosphate minerals such as variscite, strengite and hydroxyapatite would be expected to be the stable phosphate mineral phases.

As the pH of an alkaline soil increases after drying, the precipitation of the calcium phosphate minerals would follow the sequence: dicalcium phosphate dihydrate, $\text{CaHPO}_4 \cdot 2\text{H}_2\text{O}$, dicalcium phosphate anhydrate, CaHPO_4 , octacalcium phosphate, tricalcium phosphate, and hydroxyapatite. However, as discussed for flooded soils, the precipitation of hydroxyapatite is dependent on some kinetic limitation which generally results in the supersaturation of soil solutions with respect to this mineral. Fixen and Ludwick (1982) found initial soil phosphorus solubilities to be either generally clustered just below the octacalcium phosphate isotherm, or near the tricalcium phosphate isotherm. After a greenhouse crop had been grown on these soils, all soils had phosphorus solubilities which plotted below the tricalcium phosphate isotherm. The solubilities of phosphorus for the calcareous soils were clustered just below the tricalcium phosphate line, while the non-calcareous soils were generally in the hydroxyapatite solubility range. Larsen (1966) and Al-Khateeb, Raihan and Asker (1986) have reported phosphate solubilities from calcareous soils which indicated that tricalcium phosphate was the dominant form after equilibrium was reached.

Application of solubility criteria by Wright and Peech (1960) to acid soils suggested that a crystalline phosphate mineral belonging to a variscite-strengite isomorphous series was present in the soil after long-term phosphate fertilizer additions. Other workers have also proposed the presence of variscite based on solubility data from soils which received phosphorus applications (Hemwall, 1957; Lindsay, Peech and Clark, 1959; Hsu, 1964; Bache, 1964). When the aluminium activity was assumed to be controlled by amorphous aluminium hydroxide in the study discussed above by Fixen and Ludwick (1982), four of the acid soils approached soil phosphorus solubilities close to that of variscite. Lindsay et al., (1959) and Lindsay (1979) found soil solutions to be undersaturated with respect to variscite in soils which did not receive any phosphorus fertilizer, while soils which were fertilized with phosphorus had initial reaction products that were 10 to 30 times more soluble than variscite. After 18 months, the phosphorus solubilities

of the fertilized soils were found to decrease and approach that of variscite. Lindsay (1979) used this same method to evaluate the solubility of strengite where soil-Fe was assumed to be controlling the activity of ferric iron. The solubility data for the soils fertilized with phosphorus indicated that the initial reaction products were approximately in equilibrium with strengite and soil-Fe. After 18 months, however, the soil solution was undersaturated with respect to strengite indicating that the final reaction products were less soluble than strengite and was similar to soils where no phosphorus was added.

CONCLUSION

The large volume of literature that has been written on phosphorus is a tribute to the complexity of its reactions in soils and sediments. The diverse and amorphous character of initial soil reaction products challenge researchers to find innovative ways to define better that portion of the solid phase phosphorus which will be released into the soil solution and be made available for plant uptake. A better understanding of the availability of native and applied soil phosphorus to plants is needed to achieve the desired goal of greater crop production while meeting economic and environmental concerns.

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Chapter Twenty-six

CARBON AND NITROGEN DYNAMICS IN WETLAND SOILS

K.R. Reddy and D.A. Graetz

INTRODUCTION

The pore space of wetland soils is generally filled with water rather than air as in well-drained soils. Oxygen is supplied to wetland soils by diffusion through the floodwater water and through transport via the vascular system of wetland plants. Under both conditions, oxygen is supplied more slowly than the potential consumption rate. These conditions result in the development of two distinctly different soil layers: (1) an oxidized or aerobic surface layer where oxygen is present, and (2) an underlying reduced or anaerobic layer in which no free oxygen is present (Pearsall, 1950).

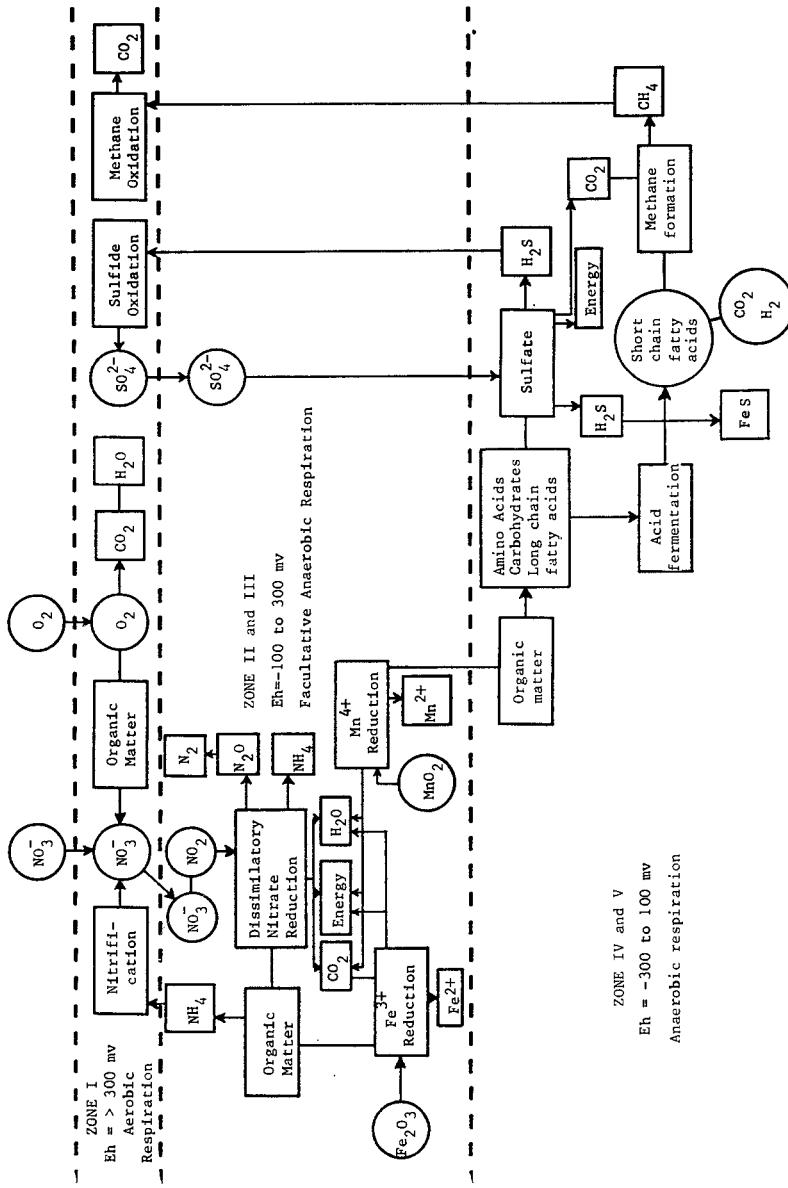
Depending on the electron acceptor availability, aerobic, facultative anaerobic and obligate anaerobic metabolism can occur simultaneously at different depths (Figure 26.1) of the wetland soil profile. Typically, in a drained soil, oxygen can be used as an electron acceptor during aerobic respiration. Upon flooding sequential reduction of electron acceptors occurs as a function of Eh (Figure 26.1). Oxygen is reduced at Eh of <300 mv, followed by the reduction of NO_3^- and Mn^{4+} at Eh of 200 mv. Iron reduction is initiated after all NO_3^- is reduced and is complete at -100mv. Sulfate reduction is initiated at Eh of >-100 mv, followed by CO_2 reduction.

Restricted gas exchange in wetland soils affects the physical, chemical and biological properties of the soils, thus altering the C and N dynamics. This chapter characterizes wetland soils with respect to electron acceptor availability, and discusses the effect of electron acceptors on C and N dynamics.

CARBON TRANSFORMATIONS

Aerobic, facultative anaerobic and anaerobic respiration pathways are presented in Figure 26.1. Detailed reviews on these pathways were presented by Yoshida (1975) and Fenchel and Jorgensen (1977). In wetland soils, aerobic respiration occurs primarily in the floodwater, aerobic soil layer (oxygen reduction zone) and in the rhizosphere of wetland plants. Soil organic C decomposition in the surface aerobic layer depends on the supply of readily oxidizable

Figure 26.1: Pathways of organic carbon decomposition in a wetland soil during aerobic, facultative anaerobic and obligate anaerobic respiration



able organic compounds and steady supply of oxygen. Aerobic decomposition of soil organic C in wetland soils is primarily regulated by oxygen supply, since C is usually not limiting. Oxygen diffusing through floodwater is rapidly consumed by microbial respiration in the first few mm of surface soil. Below this zone obligate aerobes can no longer function. The microbial community shifts to facultative anaerobic bacteria, which utilize NO_3^- , oxidized manganese compounds and then ferric iron compounds as electron acceptors.

Many micro-organisms can utilise NO_3^- as a terminal electron acceptor in the absence of oxygen. This process is called denitrification (NO_3^- to N_2O and N_2) or dissimilatory reduction of NO_3^- to NH_4^+ . Detailed reviews of this process have been reported by several researchers (Delwiche and Bryan, 1976; Stouthamer, van't Riet and Oltmann, 1980; Payne, 1981; Firestone, 1982; Reddy, Feijtel and Patrick, 1986). Significant correlations were observed between soil organic matter decomposition (expressed as CO_2 production) and denitrification, indicating the use of NO_3^- as an electron acceptor (Reddy, Rao and Jessup, 1982). No data are available on the significance of NO_3^- reduction to NH_4^+ on soil organic matter decomposition. The energy yield during NO_3^- reduction is slightly less than for oxygen reduction (Reddy *et al.*, 1986) and in order to release the same amount of energy on an oxygen equivalent basis about 1.6 times oxygen is needed if NO_3^- is used as an electron acceptor to derive the same amount of energy.

As the demand for electron acceptors increases, facultative anaerobes can also utilize manganese compounds as electron acceptors (Trimble and Ehrlich, 1970). Reduction of Mn^{4+} to Mn^{2+} occurs in moderately reduced soils ($\text{Eh} = 200$ mv) and energy yield is 67 per cent relative to the oxygen reduction. Reduction of Mn^{4+} can occur in the presence of low levels of NO_3^- (Takai and Kamura, 1966). The extent of soil organic matter decomposition by bacteria utilizing Mn^{4+} compounds depends on (1) concentration of Mn^{4+} compounds and (2) oxidizable organic matter.

As the NO_3^- is depleted, facultative anaerobes reduce Fe^{3+} to Fe^{2+} . Asami and Takai (1970) related Fe^{2+} formation to CO_2 production in an anaerobic soil amended with Fe_2O_3 . Energy yield during the enzymatic reduction of Fe^{3+} is 15 per cent of that from oxygen reduction. Soils containing a high concentration of Fe^{3+} compounds can poise Eh of the soil between -100 and 100 mv. In wetland soils, Fe^{3+} reduction occurs below the zone of NO_3^- reduction (Figure 26.1). The capacity of the Fe system in mineral soils is usually greater than the Mn system (Patrick, 1981).

Anaerobic respiration occurs in the soil zone below the Fe^{3+} reduction zone (Figure 26.1). The primary end-products of fermentation are fatty acids such as acetic, butyric and lactic acids, and the gases CO_2 and H_2 . Acetic acid is the primary acid formed in most flooded soils and sediments. Sulfate-reducing and methanogenic bacteria then utilize the end-products of fermentation and in fact depend on the complex community of fermentative bacteria to supply substrate for their metabolic activities. Both groups play an important role in organic matter decomposition and carbon cycling in wetland soil environments.

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Sulfate respiration involves utilization of SO_4^{2-} as a terminal electron acceptor by strict (obligate) anaerobes during catabolic oxidation of substrate carbon (electron donor). Although sulfate-reducing bacteria generally can utilize only a limited number of simple organic compounds, in addition to H_2 gas, it has been suggested recently that SO_4^{2-} -reducing bacteria may be 'stimulated by a large variety of organic amendments *in situ*' (Smith and Klug, 1981; Dicker and Smith, 1985).

The major pathways of methane formation are (1) reduction of CO_2 with H_2 or organic substrates (fermentation products) as electron acceptors and (2) decarboxylation of acetic acid (Yoshida, 1975). The relative importance of the two substrates, CO_2 and acetic acid, may depend on the organic loading to the sediment (Jones and Simon, 1985). In freshwater lake sediments, acetate is the dominant substrate (Winfrey and Zeikus, 1979; Strayer and Tiedje, 1978) whereas in marine sediments, CO_2 appears to be dominant as the CH_4 precursor (Claypool and Kaplan, 1974). Methane cycling in aquatic environments has been extensively reviewed recently by Rudd and Taylor (1980).

Sulfate respiration has been shown to be responsible for significant amounts of organic matter decomposition particularly in marine environments where high levels of SO_4^{2-} occur. Sulfate reduction was identified as the major form of respiration in salt marsh sediments in both Georgia and Massachusetts (Howarth and Giblin, 1983). In freshwater environments, SO_4^{2-} respiration apparently plays a lesser, but important role, in organic matter decomposition. In Wintergreen Lake, Michigan, 2.5 times as much organic C was mineralized through methanogenesis as through SO_4^{2-} reduction (Smith and Klug, 1981). Similar results were found for Lake Mendota, Wisconsin, during summer stratification (Ingvorsen and Brock, 1982). In both cases, SO_4^{2-} respiration was limited due to low amounts of sulfate.

Relative rates of sediment organic C decomposition under varying electron acceptor conditions are shown in Figure 26.2. (Reddy, 1986, unpublished results). In this study on an oxygen equivalent basis, oxygen, nitrate and sulfate were added at 450, 58 and 30 mmol/week, and these additions maintained Eh of the sediment at 312, 115 and -123 mv, respectively. Decomposition rate was highest in the oxygenated system followed by NO_3^- and SO_4^{2-} .

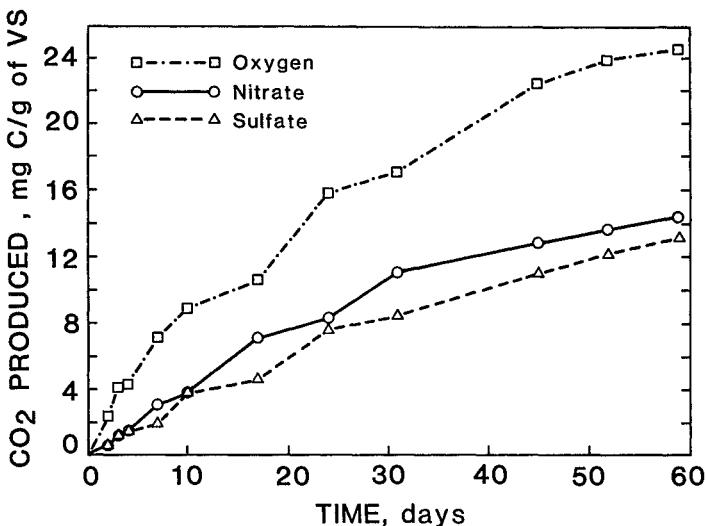
NITROGEN TRANSFORMATIONS

The major nitrogen transformations in wetland soils are presented in Figure 26.3(a,b). Detailed reviews have been presented (Focht and Verstraete, 1977; Buresh, Casselman and Patrick, 1980; Savant and De Datta, 1982; Reddy and Patrick, 1984). All N transformations are affected by the type of microbial metabolism.

Ammonification

Ammonification is the process where organic N is converted into inorganic N, specifically NH_4^+ -N. In wetland soils, mineralization rates are fastest in the oxygen zone, and decrease with depth as

Figure 26.2: Decomposition of sediment organic carbon as influenced by oxygen, nitrate and sulfate as electron acceptor source



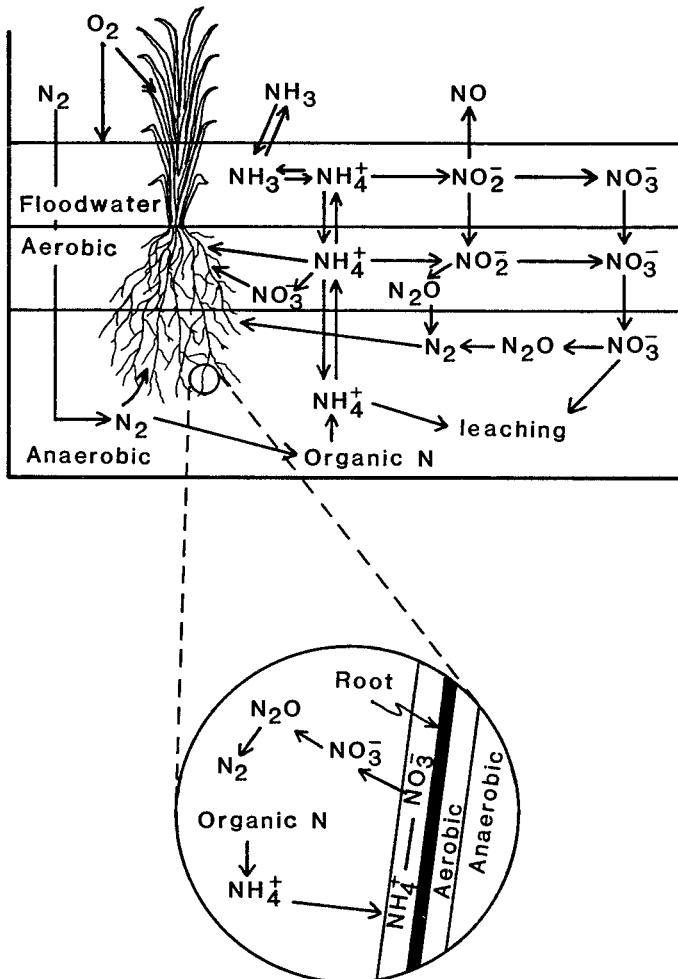
Source: Reddy, unpublished results

mineralization switches from aerobic to facultative anaerobic and obligate anaerobic microflora. Since depth of the aerobic zone is usually less than 1 cm, the contribution of aerobic mineralization to the overall N mineralization would be very small, compared to facultative anaerobic and obligate anaerobic mineralization.

Net release of NH₄⁺ during mineralization is governed by the mineralization and immobilization balance. The N requirements of aerobic bacteria are much higher than facultative anaerobic and obligate anaerobic bacteria. This can result in much higher immobilization rates in the aerobic soil layer than in the anaerobic soil layers. Mineralization of organic N to NH₄⁺ is the major process supplying N to wetland plants. Ammonium N accumulation in wetland soils was found to be rapid during the first two weeks after flooding (Ponnamperuma, 1972). Ammonium N formed during mineralization is rapidly partitioned into (1) NH₄⁺ adsorbed on the cation-exchange complex, and (2) equilibrium NH₄⁺ in soil pore water. In 38 flooded soils of Louisiana, about 20 per cent of the NH₄⁺ was in the pore water, while the remaining NH₄⁺ was found adsorbed on the exchange complex (Reddy and Patrick, 1986a). Application of external sources of NH₄⁺ can offset the equilibrium between these two fractions. The adsorptive capacity was the most influential factor in the movement of NH₄⁺ in flooded lowland rice soils (Aomine, 1978). Ammonium N in the pore water moves in two

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Figure 26.3: Pathways of nitrogen transformations in wetland soil-plant-water systems



Source: Reddy (1976). PhD Dissertation, Louisiana State University

directions, namely (1) upward movement into the overlying aerobic zone and the floodwater, and (2) movement toward plant roots. Rate of NH_4^+ movement is regulated by the concentration gradient established as a result of (1) plant uptake; (2) loss mechanisms in the rhizosphere; and (3) loss mechanisms at the soil-water interface. Other factors governing the overall process include; mineralization rate, concentration of NH_4^+ in the pore water, cation-exchange capacity, types of other cations on the exchange complex and bulk density (Reddy and Patrick, 1984).

Ammonia Volatilization

Ammonia volatilization can be very active in wetland soils, where the pH of the overlying water is above 7. Under these conditions, much NH_4^+ can be lost through volatilization. Volatilization rate is controlled by the NH_4^+ concentration in the floodwater, temperature, wind velocity, solar radiation, nature and number of aquatic plants, and capacity of the system to change the pH in diurnal cycles. Bouldin, Johnson, Burda and Kao (1974) observed losses of NH_4^+ up to 38 per cent per day and concluded that the major portion of this loss was due to NH_3 volatilization. Reddy and Graetz (1981) reported rapid NH_3 volatilization from water aerated with CO_2 -free air, whereas very little NH_3 volatilization occurred in water containing CO_2 . In floodwater containing algae, CO_2 can be depleted during photosynthesis, thereby increasing pH, and enhancing the NH_3 volatilization.

Nitrification

Nitrification can occur in the overlying water (Curtis, Durrant and Karman, 1975; Ruane and Krenkel, 1978), in the surface aerobic soil layer (Takai and Uehara, 1973; Reddy, Patrick and Phillips, 1976) and in the root zone (Reddy and Patrick, 1986b). Nitrification rate in wetland soils depends on the supply of NH_4^+ to the aerobic zone, pH and alkalinity of water, temperature, presence of nitrifying bacteria and the thickness of the aerobic soil layer (Savant and De Datta, 1982; Reddy and Patrick, 1984). In soils low in organic matter, the aerobic soil layer is usually thick (1-2 cm) and most of the nitrification occurs in this zone such that no NH_4^+ diffuses into the floodwater. In soils high in organic matter, the aerobic soil layer is thin (<0.1 cm), and under these conditions nitrification usually occurs in the floodwater.

Nitrification also occurs in the rhizosphere of wetland plants. The diffusion of oxygen from rice roots to adjacent soil creates an aerobic environment around the roots (Oremland and Taylor, 1977; Iizumi, Hattori and McRoy, 1980; Howes, Howarth, Teal and Valiela, 1981). This aerobic soil envelope around the roots can support nitrification of NH_4^+ diffused from surrounding anaerobic zones.

Denitrification

In wetland soils, denitrification occurs in the anaerobic soil below the aerobic soil layer. The rate of denitrification in this zone depends on the supply of NO_3^- , energy source, microflora and temperature. The supply of NO_3^- in wetland soils is derived by nitrification of NH_4^+ in the aerobic zone followed by the downward diffusion of NO_3^- from the aerobic zone to the underlying anaerobic zone. The flux of NO_3^- from the floodwater and aerobic soil layer into anaerobic zones is controlled by: available carbon supply (Stanford, VanderPol and Dzienia, 1975a; Reddy, Rao and Jessop, 1982), thickness of the aerobic layer (Engler and Patrick, 1974), NO_3^- concentration of the floodwater (Reddy, Sacco and Groetz, 1980), temperature (Stanford, Dzienia and VanderPol, 1975b), and mixing and aeration in the floodwater. Nitrate diffusion rate in

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wetland soils has been found to be in the range $1.2\text{--}1.9 \text{ cm}^2 \text{ day}^{-1}$, which is about seven times faster than NH_4^+ diffusion (Reddy and Patrick, 1984). Rapid diffusion of NO_3^- followed by high denitrification rate is the main cause of low NO_3^- accumulation in the floodwater/aerobic soil layer.

Nitrification and denitrification may occur simultaneously in wetland soils (Pearsall, 1950; Mitsui, 1954; Patrick and Reddy, 1976). Their significance in geochemical and ecological processes of wetland soils, estuarine and coastal marine sediments was reviewed by Kemp, Wetzel, Boynton, D'Elia and Stevenson (1982). The potential of nitrification-denitrification in the root zone of rice plants was experimentally demonstrated by Reddy and Patrick (1986b). This process accounted for an overall N loss of about 20 per cent of the applied fertilizer N.

Ammonium diffusion and nitrification limit N loss from wetland soils, whereas NO_3^- diffusion and denitrification usually occur at a rapid rate and are not likely to limit the overall process. The ultimate conversion of NH_4^+ to N_2 gas through nitrification and denitrification coupled with NH_4^+ and NO_3^- diffusion was demonstrated by Patrick and Reddy (1976) for wetland soils, and by Jenkins and Kemp (1984) for estuarine sediments. A recent study by Reddy and Patrick (1986), (unpublished results) have revealed greater N_2 flux in systems with plants than without plants.

Nitrogen Fixation

In wetland soils, biological N_2 fixation may occur in the floodwater, the aerobic soil layer, the anaerobic soil layer and the root zone (rhizosphere), and leaf and stem surfaces of plants. Buresh, Casselman and Patrick, (1980) reviewed the role of N_2 fixation in wetland soil systems. Floodwater is exposed to sunlight and is the most suitable site for autotrophic N_2 fixation. Some examples of autotrophic N_2 fixers are blue-green algae and cyanobacteria. They also grow at the aerobic soil-water interface. Depending on the population of N_2 fixers and environmental conditions a wide range of N_2 fixation rates in the floodwater have been reported (Buresh et al., 1980).

Significant rates of N_2 fixation by the heterotrophic bacteria in the anaerobic soil layer have also been reported. Nitrogen fixation by these bacteria can account for $0.1\text{--}0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, as compared to $25 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ by blue-green algae (Buresh et al., 1980).

There are large populations of N_2 -fixing bacteria present in the rhizosphere of wetland plants (Yoshida and Ancajas, 1973a,b; Bristow, 1974; Teal, Valicla and Berlo, 1979). Nitrogen fixation in the root zone of wetland plants is possible only if N_2 gas is present. Wetland plants have a transport mechanism whereby atmospheric N_2 is transported to the root zone (Yoshida and Broadbent, 1975). In addition, N_2 generated during denitrification is also potentially available for N_2 fixation.

CONCLUSIONS

A critical evaluation of the literature reveals that a better understanding of biogeochemical processes regulating C and N dynamics in wetlands is needed, both at the process level (under laboratory conditions) and the ecosystem level (field conditions). The relative roles of aerobic, facultative anaerobic and obligate anaerobic bacteria in C and N dynamics of wetland soils need to be established. Data on C and N dynamics of natural wetlands and altered wetlands are limited.

Measurements of C and N processes need to be developed in situ in a system containing soil-water-plant components. Carbon and N dynamics in the rhizosphere of wetland plants are poorly understood. Research on gaseous fluxes (CO_2 , CH_4 , N_2O and N_2) from wetlands is needed to evaluate the global cycles of C and N. Significance of C and N dynamics in the overall productivity of a wetland needs to be determined under different climatic conditions.

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Chapter Twenty-seven

THE INFLUENCE OF REDOX POTENTIAL ON THE ENVIRONMENTAL CHEMISTRY OF CONTAMINANTS IN SOILS AND SEDIMENTS

Robert P. Gambrell and William H. Patrick Jr

INTRODUCTION

Potentially toxic substances such as heavy metals, pesticides, and industrial organics that enter waterways from land runoff or waste discharge accumulate in sediments. Some of these substances are applied directly to soils as when agricultural fields are amended with sewage sludge, or when pesticides are applied. Mobility and bioavailability of contaminants, and degradation in the case of synthetic organics, affect the environmental risk associated with these toxic materials. These environmental chemistry processes are affected by the physical and chemical properties of the contaminated soils and sediments. Oxidation-reduction status, or redox potential, has received much research attention by the Laboratory for Wetland Soils and Sediments at Louisiana State University during the last 15 years. This chapter reviews some of the published and unpublished work from the laboratory during this period.

Trace and Toxic Metals

Trace and toxic metals exist in several chemical forms in surface waters, soils, and sediments, and these forms vary greatly in their relative mobility and biological availability. Forms of metals most readily available to aquatic and benthic organisms and plants include those dissolved in the soil solution, surface, and interstitial waters, and metals bound to the solid phase by cation-exchange processes. Metals fixed within the crystalline lattice of primary and secondary minerals by isomorphic substitution are unavailable to plants or animals. There are a number of chemical forms between these availability extremes that are potentially available. The metals in contaminated soils and sediments are usually in these potentially available forms. Some of the processes immobilizing metals in potentially available forms include: (a) formation of metal oxides, hydroxides, and carbonates of low solubility, (b) adsorption to colloidal hydrous oxides of iron and manganese in aerobic, neutral or alkaline pH environments, (c) precipitation as highly insoluble sulfides under strongly reducing conditions, and, (d) complex formation with dissolved and insoluble humic materials (Gambrell, Khalid and Patrick, 1980). Metals may

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undergo transformations between these forms affecting their mobility and availability due to changes in the physicochemical properties of the system such as pH, redox potential, and salinity.

Synthetic Organics

Much published information is available on the fate and mobility of many pesticides and industrial organics in soils. This work has been conducted largely on well-drained agricultural soils. However, these compounds are subjected to a wide range of physicochemical conditions in the environment. Pesticide residues, for example, usually become associated with well-oxidized, medium-textured soils after typical agricultural applications. Subsequently, these residues may be transported in dissolved or adsorbed forms to surface waters and sediments of streams, rivers, lakes, and estuaries where the environmental chemistry conditions and biological populations are very different from the conditions at the application site. In particular, compared to typical agricultural soils, sediments are usually characterized by higher clay and organic matter contents, a narrower pH range, and moderate to strongly reducing conditions (Gambrell, Khalid and Patrick, 1978). The persistence and fate of organic pesticide residues and industrial organics released into the environment, and subsequently the potential environmental impact of these materials, is influenced by the physicochemical conditions of the receiving soils and sediments.

EXAMPLES OF RESEARCH FINDINGS

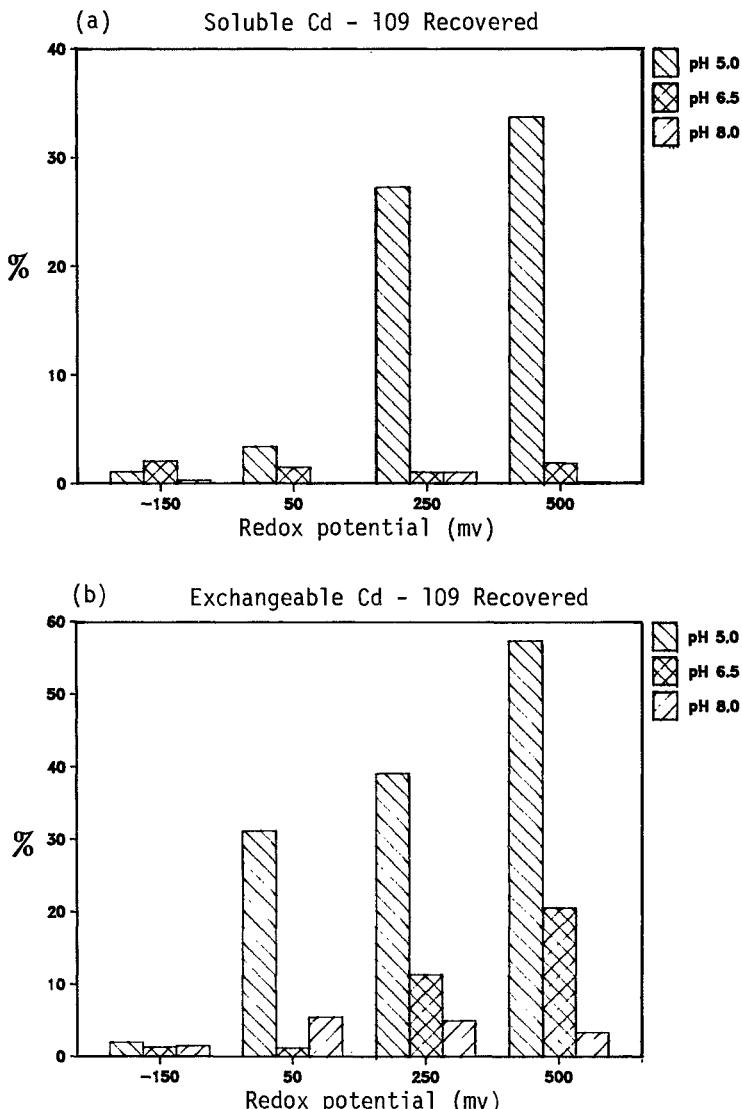
Trace and Toxic Metals

Laboratory chemical availability studies. Numerous laboratory studies have been conducted at LSU on the influence of soil or sediment pH and redox conditions on levels of trace metals in various chemical forms. Important physicochemical effects on the transformations of Fe, Mn, Cu, Zn, Cd, Pb, and Hg have been found. Because of the high potential toxicity of Cd, its relative mobility, and the affects of redox potential on its biological availability, this paper considers only Cd. However, although Zn responds like Cd to changes in redox potential, other metals show substantial differences in how their chemistry is influenced by the physicochemistry of soils and sediments (Gambrell, *et al.*, 1980; Gambrell, Khalid, Verloo and Patrick, 1977).

Figure 27.1(a) indicates the levels of water-soluble labeled Cd-109 recovered from a Mississippi River sediment incubated under controlled pH and redox potential conditions. Figure 27.1(b) presents exchangeable levels (1 N sodium acetate extractable) sequentially extracted from the same sediment. Under both moderately acid (pH 5.0) and near-neutral conditions, it is apparent there was much more exchangeable Cd under oxidizing conditions compared with reducing conditions (a redox potential of -150 mv represents strongly reducing conditions and +500 mv represents strongly oxidizing conditions).

The above work used a sequential extraction procedure to examine pH and redox potential effects on levels of metals in

Figure 27.1: The effect of controlled pH and redox potential on labeled Cd recovered in dissolved (a) and exchangeable (b) forms in a Mississippi River sediment material



Source: Khalid, Gambrell and Patrick (1981)

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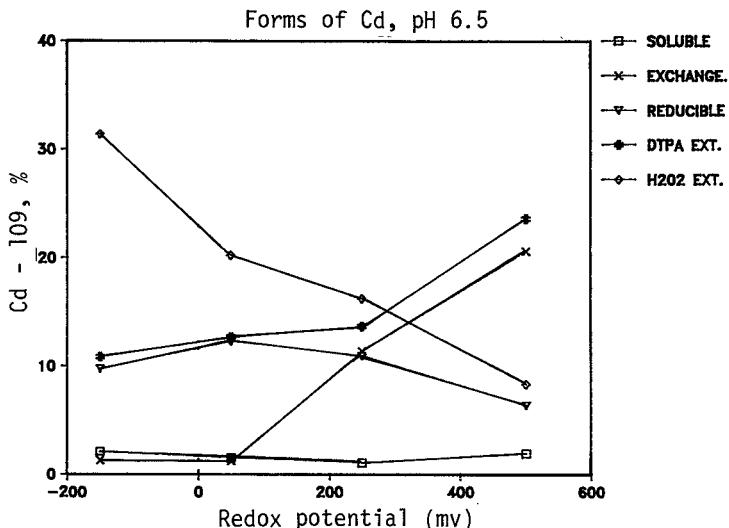
various chemical forms as well as transformations between these forms as a consequence of altering pH and redox potential. In addition to (1) soluble and (2) exchangeable forms, (3) oxalic acid-ammonium oxalate extractable metals (associated with hydrous oxides), (4) DTPA-extractable metals (relatively weakly associated with large-molecular-weight humic acids), and (5) acid/hydrogen peroxide-extractable metals (strongly bound by sulfides and/or large-molecular-weight humic acids) were measured. Figure 27.2 shows the effects of redox potential on the recovery of labelled Cd in the five chemical forms studied from the Mississippi River sediment incubated at pH 8.0. Little was found in the dissolved form at this pH, but the effect of redox potential on the readily available exchangeable form was apparent as redox potential increased from 250 to 500 mv. Only a moderate proportion of the Cd was associated with the iron oxide fraction. The 0.1 N DTPA extract used in this sequential fractionation procedure removed some of the metals weakly bound to the large-molecular-weight humic materials. Cadmium thus became more easily extractable from insoluble humic materials as the initially anaerobic sediment was oxidized. Levels of Cd in the hydrogen peroxide-extractable fraction decreased with increasing redox potential. These data suggested most of the Cd was strongly bound to the large-molecular-weight humic material fraction under anaerobic conditions. However, as the sediment became better oxidized, Cd began to appear in less strongly bound forms. Precipitation as insoluble CdS at -150 mv was not a significant immobilizing process for the Cd since the Mississippi River sediment material contained insufficient sulfides for this to be a factor (Gambrell et al., 1977).

Laboratory and greenhouse plant availability studies. The above work represents chemical availability studies. Increasing soluble and exchangeable Cd with increasing redox potential indicates that Cd uptake by plants is greater from oxidising soils or sediments than reducing materials. Laboratory and greenhouse studies have been conducted to test this hypothesis.

Figure 27.3(a) and (b) shows the labelled Cd content in stem plus leaf tissue in laboratory-grown Spartina alterniflora and Spartina cynosuroides where the roots were suspended in an aqueous soil slurry amended with labelled Cd and maintained under controlled pH and redox potential conditions (Gambrell, Collard and Patrick, 1980). It is clear that moderately acid, oxidizing conditions resulted in greater uptake of labelled Cd by the plants. The R^2 between labeled tissue cadmium content and labeled Cd extracted from the rooting medium with 1 N sodium acetate was 0.924 and 0.850 for S. alterniflora and S. cynosuroides, respectively (both significant at the 1 per cent level).

Greenhouse studies were conducted using a Cd-enriched, unstirred rooting medium where pH was measured, but not controlled, and three soil redox conditions were maintained by measuring redox potential daily and manually controlling the soil water content (Gambrell et al., 1980). These results (Figure 27.4(a) - (b)) again demonstrate the increased plant availability of Cd as soil or sediment becomes more oxidizing. In this greenhouse

Figure 27.2: The effect of redox potential and levels of labeled Cd in various chemical forms in a Mississippi River sediment material incubated at pH 6.5



Source: Adapted from Khalid et al. (1981)

study where soil pH was not controlled, the pH decreased with oxidation. This is common in non-calcareous soils (Gambrell and Patrick, 1978). Thus oxidizing this soil results in a pH interaction that also favours enhanced Cd uptake by the two marsh grass species.

Subsequent to the above Cd uptake studies, Simmers, Folsom, Lee and Bates, (1981) expanded this work in a greenhouse study examining Cd uptake by Cyperus spp. Sediments from 15 sites were used and plants were grown under simulated upland and flooded conditions. With one exception, more Cd was taken up from the 15 sediments under simulated upland disposal conditions than under flooded reducing conditions.

Recent work (Gambrell, Patrick, Landes and Reddy, 1983) has also shown that the Cd content of corn and rice is greater when grown in aerobic, sludge-amended soils than in the same sludge-amended soils maintained under anaerobic conditions.

Applications of research findings. The research described above demonstrated greater mobility and biological availability of Cd in oxidized soils and sediments compared to reducing or anaerobic systems. As an example of how information of this type might be

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Figure 27.3: The effect of oxidation conditions and controlled pH on uptake of labeled Cd by (a) Spartina alterniflora and (b) Spartina cynosuroides in soil suspensions, Laboratory Microcosm Study

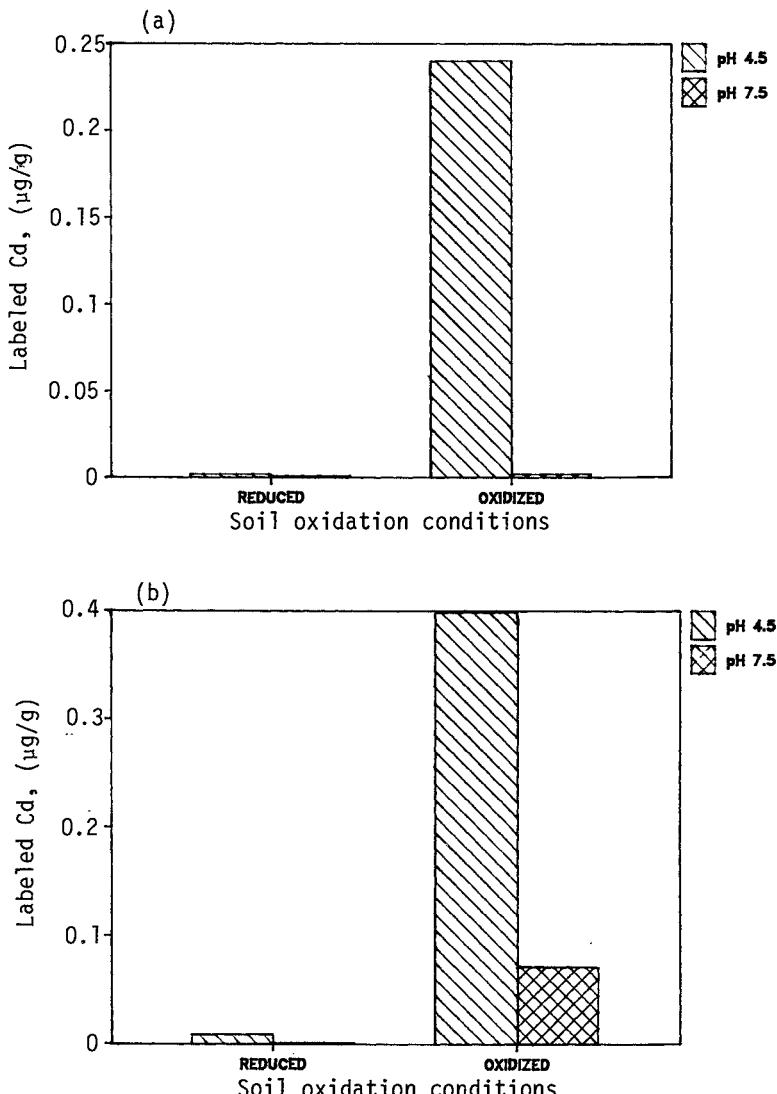
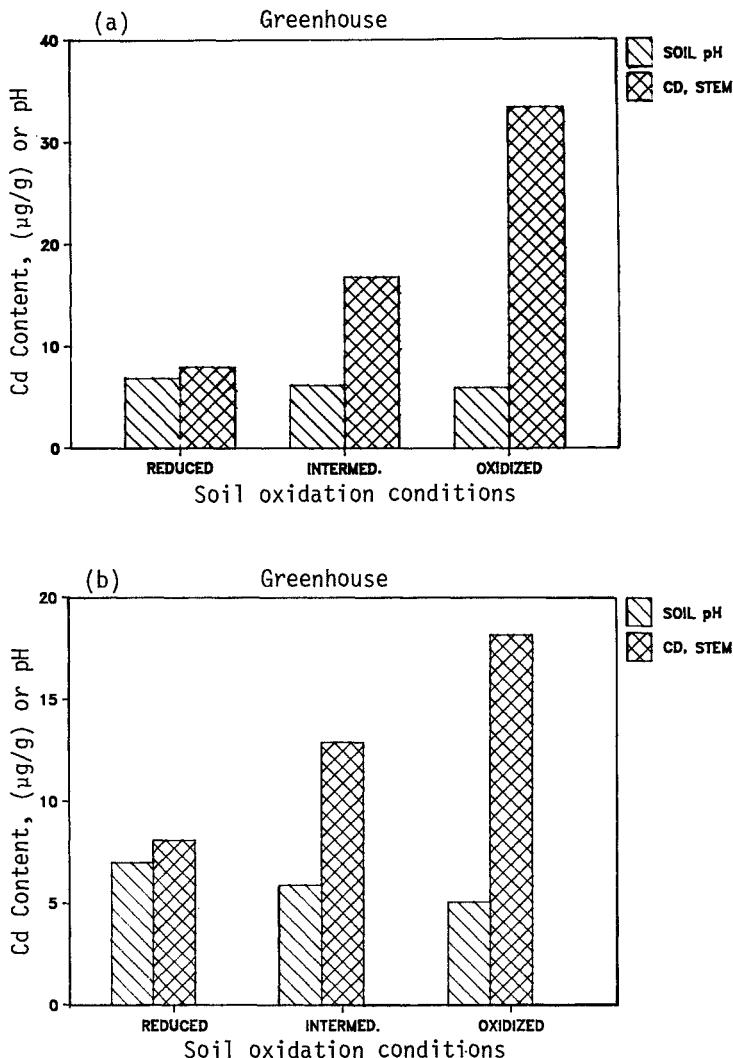


Figure 27.4: The effect of soil oxidation conditions on the Cd content of (a) Spartina alterniflora and (b) Sorghum halepense and soil pH in a Cd-amended soil, Greenhouse Study



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used, the following paragraphs will consider selection of a disposal method for a typical, fine-textured, anaerobic sediment contaminated with Cd. Gambrell et al. (1978) present a detailed discussion of the many possible disposal options for a dredged material. However, depending on the amount and type of contaminants present and other site-specific factors, some disposal alternatives are more environmentally sound than others. The optimum disposal method for a dredged material highly contaminated with Cd would be underwater placement in a low-energy (slow flow) hydraulic regime. The still water overhead should prevent gradual dispersion of contaminated solids. Stable underwater mounding also contributes to the maintenance of the pH and oxidation-reduction conditions favouring the immobilization of Cd in various solid phases. However, long-term burial may require water depths of 30 meters or more to prevent dispersal of the mound during storms. Thus, environmentally optimum disposal methods are often not available as sufficiently deep water columns are often not conveniently located.

In slow flowing water, capping with clean sediment further decreases the risk of Cd accumulation by benthic organisms that colonize the site. Also, capping contributes an additional anaerobic, cadmium-immobilizing sediment layer that should further isolate the contaminated material. Where contamination levels are not high and stable mounding can be achieved, subaqueous disposal without capping may be appropriate.

Intertidal disposal for marsh development with capping by clean sediment material may sometimes be an environmentally acceptable alternative. Intertidal disposal will generally maintain the long-term, anaerobic conditions favouring immobilization of Cd. A boundary structure (containment wall) may be necessary to prevent gradual erosion and dispersion of contaminated sediments, and capping with clean sediments reduces access to the contaminated zone by plant roots and benthic animals.

Upland disposal can also effectively immobilize Cd, but only under rigorously imposed conditions. For example, the disposal zone should be underlain by a water-impermeable barrier to help in maintaining continuous flooding conditions. Though environmentally acceptable, economic and technological restrictions of initial site development and long-term maintenance make this a very unattractive alternative, or, at best, an alternative of last resort. Except for the rigorously controlled disposal described above, most other upland applications would pose a high potential for plant uptake of excessive Cd or contamination of nearby surface and groundwater due to the increased mobility of Cd.

For a highly contaminated dredged material, subaqueous disposal in water that sometimes has a high flow rate would not immobilize the Cd. Contaminated particulates would gradually be transported over a wide area as the subaqueous mounds eroded. Also, chemical transformations of Cd could occur during transport of contaminated particulates in an oxidized water column, or at an oxidized sediment-water interface, increasing the potential for release and biological accumulation of Cd. Intertidal disposal in a fast moving water environment would also result in erosion of contaminated particulates. If capping with clean sediments were not

done, there would be additional potential for transport via plant uptake.

Table 27.1 summarizes the various disposal options and relative environmental risks for a Cd-contaminated sediment. A much more thorough treatment of disposal options is given by Gambrell et al., (1978)

Synthetic Organics

During the last 10 years, the effects of soil and sediment redox potential has been studied on about 20 synthetic organic compounds (insecticides, herbicides, industrial organics) and petroleum hydrocarbons in this laboratory. A few results of these studies will be briefly summarized below, followed by a reference to a recently completed case history in which the conclusions regarding a long-term environmental assessment depend in part on degradation of an insecticide residue in various redox environments in field soils, drainage ditches, and sediments of a lake watershed.

Table 27.1: Selection of a disposal alternative for a Cd-contaminated dredged material

Example conditions: fine textured, anaerobic sediment, moderately to highly contaminated with Cd

Optimum

- Subaqueous:
 - Achieve stable mounding (i.e. low-energy water with capping by clean sediments)
 - Confined in a depression with capping by clean sediments

Acceptable

- Subaqueous:
 - Achieve stable mounding without capping (may be acceptable under some conditions)
- Intertidal:
 - Confined by boundary structure with capping by clean sediments
- Upland:
 - Long-term confinement under ponded (flooded) conditions

Unacceptable

- Subaqueous:
 - Unconfined deposition in a high-energy water column
- Intertidal:
 - Unconfined habitat development
- Upland:
 - Agricultural soils amendment
 - Habitat development
 - Others

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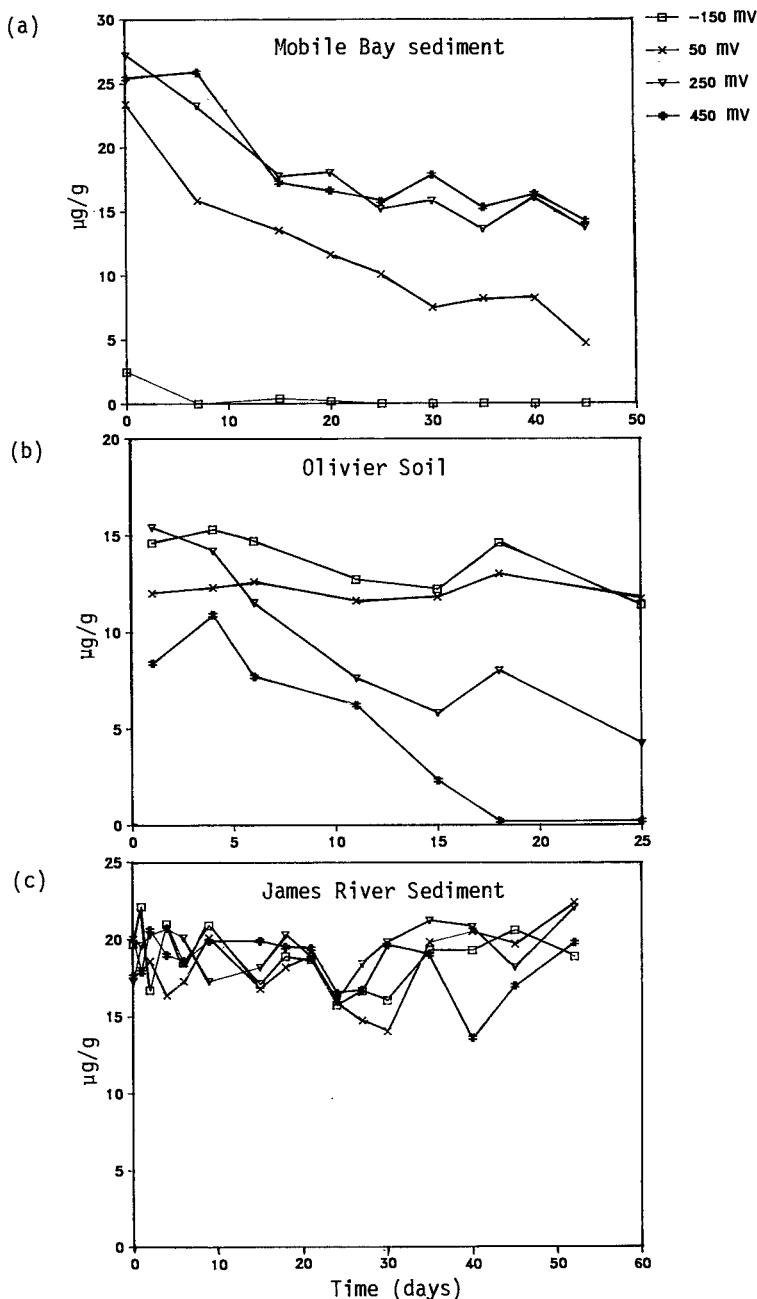
Laboratory studies. Figure 27.5(a) gives the levels of DDT in a Mobile Bay sediment suspension incubated at pH 8.0 and four redox potential levels ranging from strongly reducing (-150mv) to well oxidized (+450mv). The sediments were initially amended with 25 µg/g DDT in the laboratory incubation vessels, then sediment aliquots were periodically removed, extracted and analyzed for DDT by gas chromatography (Gambrell, Reddy, Collard, Green and Patrick, 1984b). In these studies, essentially all of the DDT was degraded within a very few days under strongly reducing conditions, whereas the DDT was much more persistent under the two highest redox potential treatments.

Not all synthetic organic compounds degrade more rapidly under anaerobic conditions like DDT. Figure 27.5 also indicates the effects of redox potential on the degradation of the insecticides permethrin and kepone. Unlike DDT, permethrin was found to degrade more rapidly in an agricultural soil under oxidizing conditions. However, the oxidation-reduction status of James River (VA) sediment had no apparent effect on the persistence of kepone in the laboratory studies (Gambrell et al., 1984b). The degradation rates of all but two of the approximately 20 synthetic organic and petroleum hydrocarbons examined to date in this laboratory have been influenced by soil or sediment oxidation-reduction conditions.

In typical surface soils and sediments, the adsorption of synthetic organics is usually controlled to a large extent by the large-molecular-weight humic materials, or organic matter content (Reddy and Gambrell, 1986). Also, hydrous oxides of iron and manganese may play a role in the immobilization process (Pionke and Chesters, 1973). Both the chemical nature and amount of organic matter and hydrous oxides are affected by the redox environment with which these soil components become associated. Table 27.2 indicates the effects of redox potential on the adsorption of PCP (pentachlorophenol) on a sediment from the Mississippi River Gulf Outlet, southeast of New Orleans, where a major spill of PCP occurred in 1980. The adsorption coefficients were greater for this compound when equilibrated with oxidized channel sediments. Knowledge of redox effects on the strength of partitioning of synthetic organics with the sediment solid phase could be useful in evaluating the mobility and fate of compounds at contaminated sites.

Case study. Fish in Lake Providence in northeastern Louisiana have been known for a number of years to contain excess levels of DDT, DDE (its degradation product) and toxaphene long after these insecticides were banned. Certain types of fishing were banned in the mid-1970s. Though the ban was lifted on all but one species in 1982, fish tissue residues continue to hover around the US Food and Drug Administration's alert levels of 5 µg/g. This problem generated interest in the processes affecting the fate of the insecticide residues in the lake and watershed, the pathways for the residues getting into fish, the length of time before the residues would degrade to acceptably low levels, and possible management practices to enhance the rate of improvement in the lake system. Field sampling and laboratory work were conducted to

Figure 27.5: The effect of redox potential on recovery of (a) DDT, (b) permethrin and (c) kepone from spiked soil and sediment suspensions



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Table 27.2: Adsorption coefficients for an estuarine sediment amended with pentachlorophenol and treated to achieve oxidized and reduced conditions

Sediment oxidation conditions	Sediment pH	Adsorption coefficient at equilibration time	
		2 hour	24 hour (K values)
Reduced	6.8	77a	117a
Oxidized	6.8	111b	170b

Means within each column not followed by the same letter are significant at the 5% level using Duncan's Multiple Range procedure

Source: Adapted from DeLaune, Gambrell and Reddy (1983)

try to answer some of these questions (Gambrell and Patrick, 1984; Gambrell, Reddy, Taylor, and Patrick, 1984c).

Extensive residue surveys of the agricultural soils of the watershed and the sediments of drainage ditches, streams, and the lake, as well as sediment transport measurements, indicated the source of the contaminants in the fish was the frequent transport of fresh residues into the lake from surface runoff and erosion rather than accumulation and recycling of residues between the lake mud and surface waters. Once the residues become associated with the anaerobic lake sediment, degradation was believed to be sufficiently rapid to degrade most residues within a few weeks or months.

Table 27.3 indicates the levels of toxaphene and total DDTs (DDT, DDD and DDE) in various watershed components going down the drainage sequence from agricultural soils, to field ditches, stream sediments, and finally lake sediments. It is apparent that there is a sequential decrease in residue levels as the contaminated soil particulate phase is transported down the drainage sequence from fields to the lake.

The data in Table 27.3 do not accurately reflect the enhanced degradation of these chlorinated hydrocarbon residues in the more anaerobic soil and sediment components of the watershed. It is reasonable to expect that there is some segregation of the soil solid phase during the erosion process such that some of the larger sand and silt particles drop out of the solids being transported. As a result the solid phase reaches the lake more enriched in clay content than the agricultural soils in the fields from which the sediments are derived. Since such materials as trace and toxic metals and pesticides are more strongly associated with the finer particles, it is reasonable to expect the solid phase actually reaching the lake to be enriched in DDT and toxaphene above levels reported for the agricultural soils. Evidence for this was obtained during one large runoff event where bulk water samples were

Table 27.3: Total DDTs and toxaphene levels in field soils, field drainage channels, stream sediments and lake sediments

Watershed component	Compound	Mean ($\mu\text{g/g}$)	Standard deviation	Number of samples
Field soils	Total DDTs	0.89	0.72	33
Field ditches	Total DDTs	0.71	0.66	7
Stream sediments	Total DDTs	0.31	0.19	6
Lake sediments	Total DDTs	0.28	0.21	41
Field soils	Toxaphene	1.78	1.34	33
Field ditches	Toxaphene	0.80	0.74	7
Stream sediments	Toxaphene	0.17	0.15	6
Lake sediments	Toxaphene	0.18	0.17	41

Source: Adapted from Gambrell *et al.* (1984c)

obtained from the two major streams entering the lake. Suspended particulates were separated by centrifugation and analyzed for the two pesticides of interest (Table 27.4). It was found that DDT and toxaphene levels in the suspended particulates transported to the lake during this runoff event were 2 to 3 times the levels found in the field soil samples.

It was concluded that the frequent input of fresh DDT, DDE and toxaphene from the field soils during frequent runoff events was the primary source of residues finding their way into fish tissues. Long-term sediment accumulation and concentration of residues that later exchanged with and moved into the surface water and the food chain were not the problem.

With this point established, and with the other information obtained on the transport and fate of these residues in the watershed, it was possible to estimate how long these residues will

Table 27.4: DDT+DDE and toxaphene in the suspended particulate phase in Jack Falls Bayou and Bayou Providence during a major runoff event on 13 April 1983

Stream	Sediment load (g/l)	DDT	Toxaphene ($\mu\text{g/g}$)
Jack Falls Bayou	0.45	2.7	6.7
Bayou Providence	0.48	2.8	3.5

Source: Adapted from Gambrell *et al.* (1984c)

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continue to be a problem and the probable value of proposed remedial actions. At the time of this study, at least one small diversion project had been completed diverting field drainage away from the lake. Additional diversion projects are under consideration. Such projects are expensive, however, and at best, can be applied to only a small percentage of the watershed.

Though DDT and toxaphene degrade more quickly under reducing than oxidizing soil conditions, there is some loss of these materials with time in oxidized soils. A second field survey of the residue levels conducted two years after the first indicated field levels decreased about 20 per cent in two years (Gambrell and Patrick, 1984). The findings of the study suggested that if no remedial action were attempted, the DDT and toxaphene residues would decrease to well below health alert levels in another decade or less. (It should be mentioned that this situation probably existed for well over a decade prior to the fishing ban with residue levels higher than currently found.) If it is decided to accelerate the improvement of residue levels, conscientious application of recommended soil conservation practices is the most cost-effective management method to speed the decline in residue levels in fish. Expensive diversion of some watershed field drainage around the lake may be difficult to justify.

CONCLUSIONS

The oxidation-reduction status of soils and sediments has been shown to influence strongly the mobility and plant availability of trace and toxic metals as well as the persistence or degradation of synthetic organic compounds such as pesticides and industrial organics. Knowledge of how redox conditions affect the environmental chemistry of contaminants will enable better predictions of the fate and potential hazards of toxic materials in soils, sediments, and water, and should be useful in evaluating the environmental protection offered by various disposal options for contaminated soils and dredged sediments.

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Chapter Twenty-eight

WETLAND SOILS WITH HIGH SULFIDE CONTENTS

Leendert J. Pons

INTRODUCTION

Wetland soils with high sulfide contents occur worldwide in coastal plains, and in estuaries. The sulfides, mainly pyrites, have accumulated because the reduction products of sulfates (supplied by sea water) react with iron oxides (present in sediments), in an anaerobic environment (inundated wetlands), in the presence of organic matter (produced by the roots of the tidal marsh vegetation)(Pons, van Breemen and Driessen, 1982).

This chapter will discuss some examples of wetlands from different climates, and identify common characteristics so that both the occurrence of pyritic muds as well as that of the resulting acid sulfate soils can be explained.

In the coastal area of Guinea-Bissau recent studies (Pons, in preparation) have shown clear relationships between geomorphological landscape features and potentially acid and non-acid muds. Similar relations occur on the coasts of South America, the Netherlands and Vietnam.

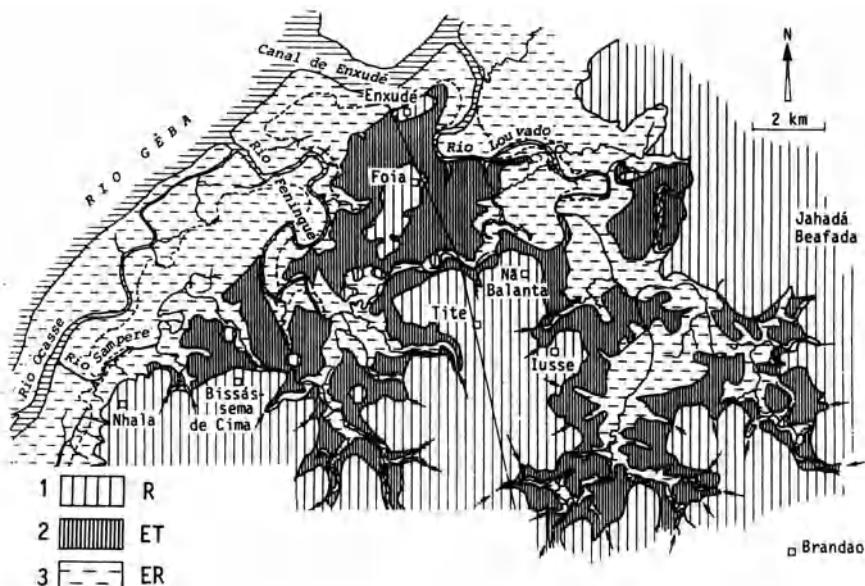
The classification of the resulting acid sulfate soils as well as their suitability for agriculture, forestry and wildlife are discussed.

SULFIDIC MUDS AND ACID SULFATE SOILS IN THE MANGROVE WETLANDS OF GUINEA-BISSAU

The ria coast of Guinea-Bissau in West Africa has a number of estuaries penetrating deep inland. Some of these are nearly filled with clay sediments while others are empty. The clay sediments include mainly kaolinitic clay minerals with some mica and smectites and do not contain carbonates (Pons, 1985).

Three different sediments have been distinguished (Pons and Ghitulescu, 1986), which are arranged into two main deposits, the Iusse and Nabalanta deposits, shown in Figure 28.1. They contain different amounts of pyrites.

Figure 28.1: The landscape and deposits of the Tite-Bissassemá project area (south of Bissau). 1. The Residual landscape (R). 2. The sub-landscape of the Estuarine Terrace (ET) with the Iusse deposits. 3. The Recent Estuarine sub-landscape (ER) with the Nabalanta deposits.



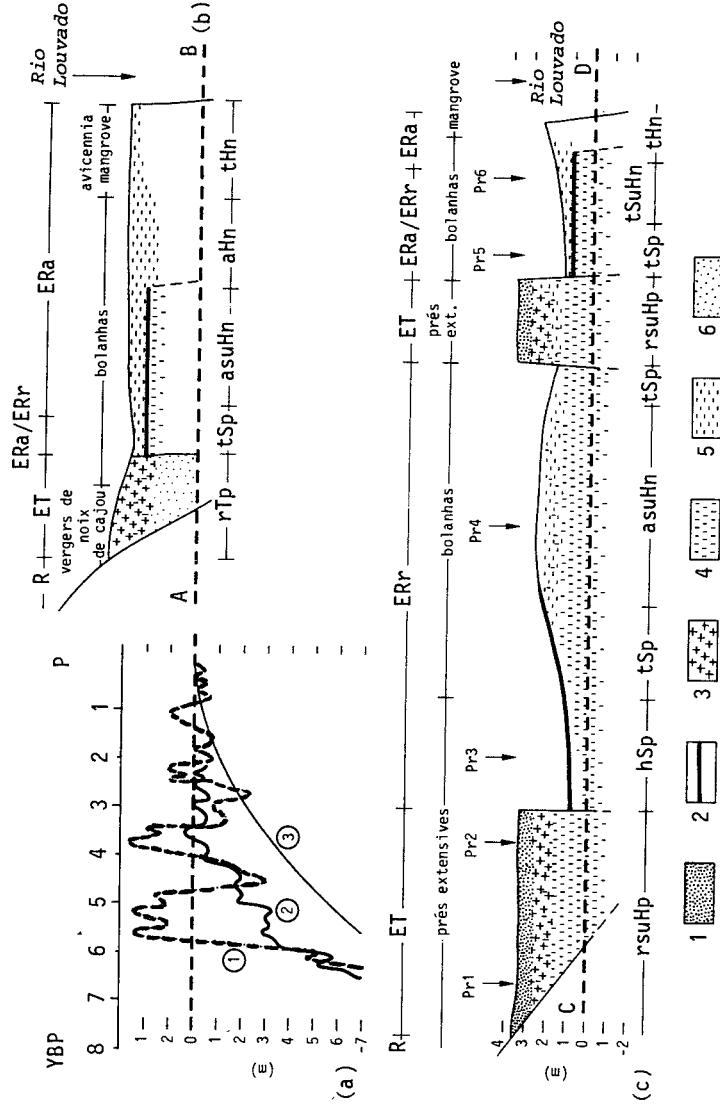
Iusse deposits

Iusse deposits are about 5,500 years old (identical with the Nouackchotean of Michel, 1973) and are now forming a marine/estuarine terrace, 1-2 m above the present sediments. Figure 28.1 shows the present extent of this terrace in an area around Tite, region Quinará, Guinea-Bissau.

After the sea attained a maximum level approximately 2 m above the present level, it fell to 1 m below the present level (Figure 28.2). Inland, freshwater creeks cut deep valleys and later, with renewed rising sea levels, tidal creeks laterally eroded important parts of the terrace (Figure 28.1).

The Iusse deposits were laid down in a 'Rhizophora sedimentation facies' under Rizophora mangroves (Rizophora mangle and Rizophora racemosa), which provided the lower-lying and strongly reduced muds with organic matter. This type of sedimentation is mainly 'vertical' (Brinkman and Pons, 1968), which permits a long-term mangrove vegetation to remain while much pyrite accumulates. After 5,500 BP, the drop in sea level caused deep drainage and oxidation and desalinization of the sulfidic muds, giving rise to Rhodic Sulfaquepts, Sulfic Rhodic Tropaquepts and

Figure 28.2: Changes in sea level, estuary deposits, soil and land utilization near Enxudé and Nabalaná (central Guinea-Bissau). (a) Eustatic curves: 1: according to Fairbridge (1961); 2: according to Morner (1969); 3: according to Jelgersma (1966). (b) Cross section Enxudé. (c) Cross section Nabalaná. 1 - Ah; dark humose topsoil; 2 - fossil vegetation horizon; 3 - red mottled; 4 - yellow mottled; 5 - brown mottled; 6 - brown mottled. R: Residual; ET: Estuarine Terrace with Iusse deposits; ER_r: Nhalá sediments; ERA: Enxudé sediments; ER_r + ERA together: Nabalaná deposits



Humaquepts. The soils are extremely infertile and strongly acid, practically impermeable when wet and very hard under dry conditions and are not used for crop production. Natural vegetation is a poor savannah forest, but burning has produced a grass-covered plain without trees.

Nabalanta deposits

The Nabalanta deposits, younger than 5,500 years may be divided into at least two different sediment units.

Nhala-phase sediments. These 2,000-4,000 year-old sediments were originally highly sulfidic muds, laid down somewhat lower than the present sediments. They have filled the eroded parts of the estuarine terrace and extended beyond the original limits of that terrace (Figures 28.1 and 28.2).

The high pyrite contents of most of the Nhala sediments result from sedimentation conditions, similar to those of the Iusse deposits. From these Nhala sediments, mainly physically unripe sulfaquepts with a sulfuric horizon (and, if saline, halic sulfaquepts) have developed. Locally better soils formed where muds have lower pyrite contents, e.g. pseudo acid sulfate soils (PASS) and even non-acid marine soils (NAMS)(aeric tropaquepts and humaquepts).

Enxudé-phase sediments. During the last 500 years the Enxudé sediments have been laid down under present sea-level conditions. In sediment-rich estuaries, the rate of this sedimentation is intense and typically 'lateral' (Brinkman and Pons, 1968) and the sediments are laid down in an Avicennia facies. Figure 28.3 shows an example near Tite, along the sediment-rich Rio Gêba, where the mangrove wetlands include narrow zones of Rhizophoras and large areas with Avicennias which enclose very saline 'tannes' (areas without vegetation)(Marius, 1984). Sediments with an Avicennia facies are only slightly influenced by the rapidly shifting mangrove zones and accumulate few pyrites.

The Enxudé sediments show initial soil development, under Avicennia mangroves as well as in areas constructed by rice farmers and locally named 'bolanhas'. They developed saline, brown-mottled non-acid alluvial soils, which form very suitable soils for rice cultivation if properly desalinized (salic or hydric tropaquepts).

THE GUIANA COASTAL PLAIN

Clay sediments of the Guiana coastal plain in South America, originating from the Amazon river, are laid down on tidal flats and in mangrove swamps. Brinkman and Pons (1968) distinguished the young Pleistocene Coropina Series and the Holocene Demerara series (Figure 28.4). The latter were divided into the Older Holocene Mara and the Younger Holocene Coronie deposits.

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Figure 28.3: Mangroves and 'tannes' near Tite-Bissassema (south of Bissau). (a) Cross section of a mangrove area, perpendicular to a creek. (b) Avicennia and Rhizophora mangroves, 'tannes' and bolanhas

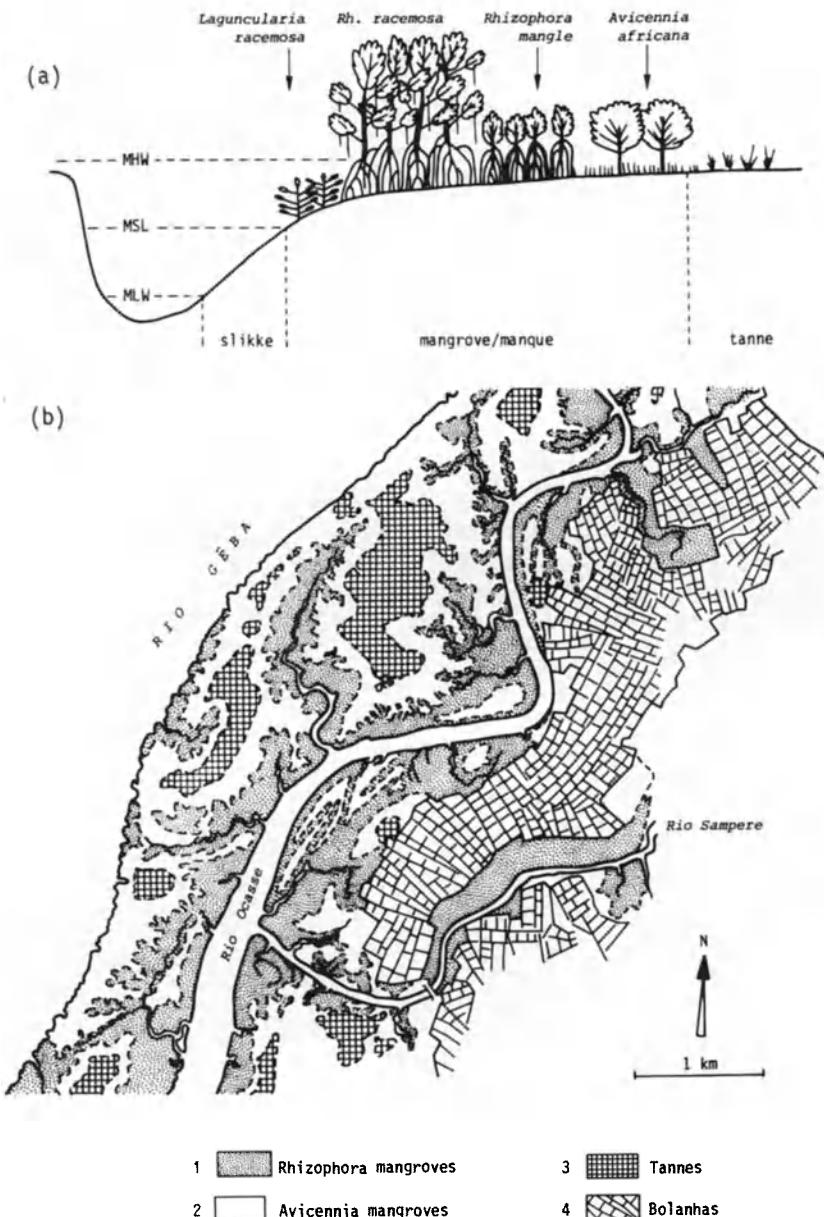
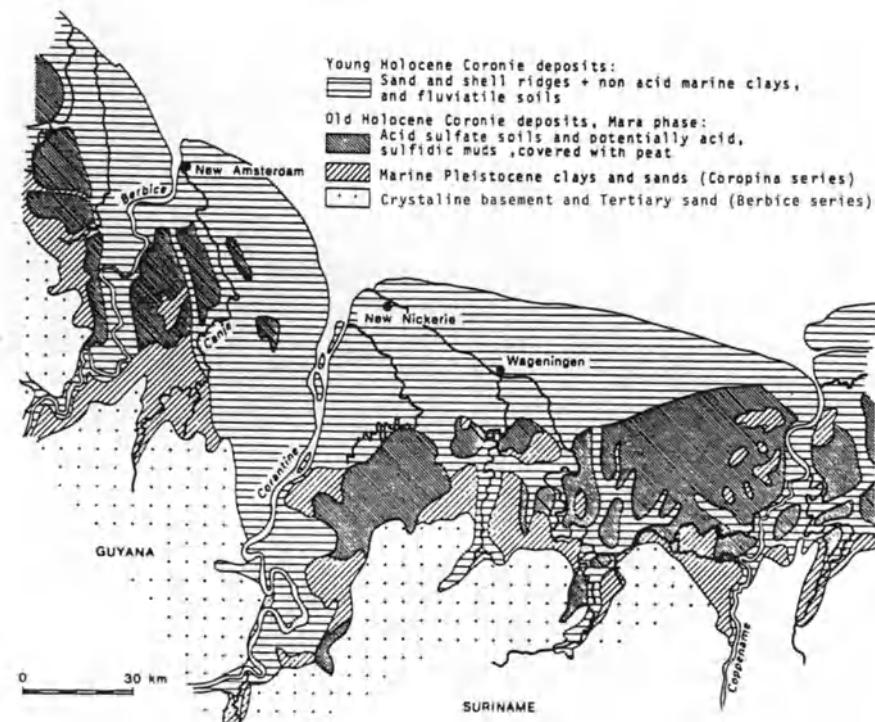


Figure 28.4: Distribution of the Old Holocene (Mara-phase) deposits (muddy clays, Rhizophora facies, rich in pyrite, vertically aggraded, partly covered by shallow peat layers) and the Young Holocene (Wanica-, Moelson- and Commowine-phase) deposits (muddy clays, Avicennia facies, poor in pyrite) laterally aggraded in western Surinam and eastern Guiana



Mara deposits

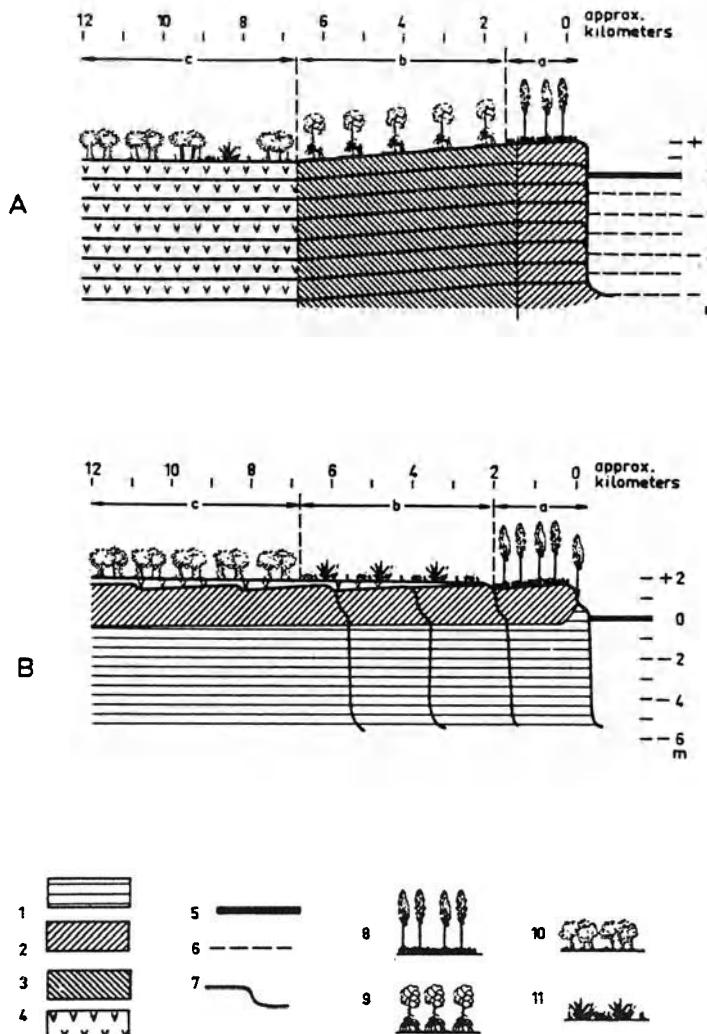
These deposits, occurring in the interior of the coastal plain (Figure 28.4) are considered to be more than 6,000 years old and include very thick layers of highly pyritic, potentially acid clays and clayey peats (Roeleveld, 1969), both in Rhizophora facies.

In the eastern and central part of the coastal plain the top of the deposits reaches to about the same level as the young Holocene Coronie deposits, suggesting a constant sea level after the maximum level about 6,000-5,500 years ago. The Mara deposits represent typical 'vertically' deposited sediments, vegetated for a long time with Rhizophora mangroves (Figure 28.5). They do not contain carbonates.

Because the deposits are poorly drained, covered with peat, and in a wet climate the soils have not developed physically or chemically and the desalinization is complete.

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Figure 28.5: Schematic cross section of slowly vertical aggradation of clays or peaty clays, rich in pyrite (Rhizophora facies) (A) and rapidly lateral aggradation of clays, poor in pyrite (Avicennia facies) (B) along the Surinam coast. A: rising sea level; B: stable sea level. 1: tidal flat clays, fine laminated, without root channels; 2: clays, poor in pyrite, Rh.-facies; 4: eustatic peat; 5: present mean sea level; 6: former sea levels; 7: successive sedimentation surfaces; 8: Avicennia; 9: Rhizophora; 10: fresh water swamp trees; 11: grasses, etc. of fresh and brackish water swamps



Coronie deposits

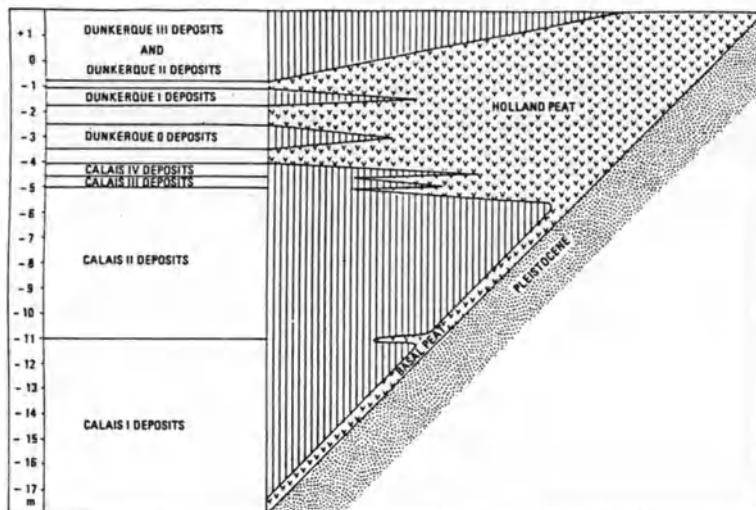
In contrast with the Mara deposits, the Coronie deposits are shallow, formed by relatively high built-up mudflats that are growing laterally rapidly (Figure 28.5). Their *Avicennia nitida* mangroves after one generation (20-30 years) are replaced by freshwater swamp forests. The *Avicennia* facies clays are low in pyrite and have a low potential acidity.

The Coronie deposits are subdivided into three different types of sediments, all *Avicennia* facies clays. From youngest to oldest they are the: Commowine-, Moleson- and Wanica-phases. Concomitantly, the soils became physically and chemically more ripened (matured) and desalinized. They evolve from Salic Aeris Hydraqents to Tropaquepts and Humaquepts. Few Sulfaquents are found.

WESTERN NETHERLANDS

In the Netherlands extensive deposits of sulfidic muds occur in different sediment units. Most of the sulfidic muds are covered by peat or by younger, non-sulfidic muds. In the central coastal area, peats may have eroded or have been excavated and the resulting lakes transformed by pumping and empoldering into deep polders. One of these sediment units locally very sulfidic, with its upper layers at -4 m (Figure 28.6), has been drained and is used for grassland of poor quality.

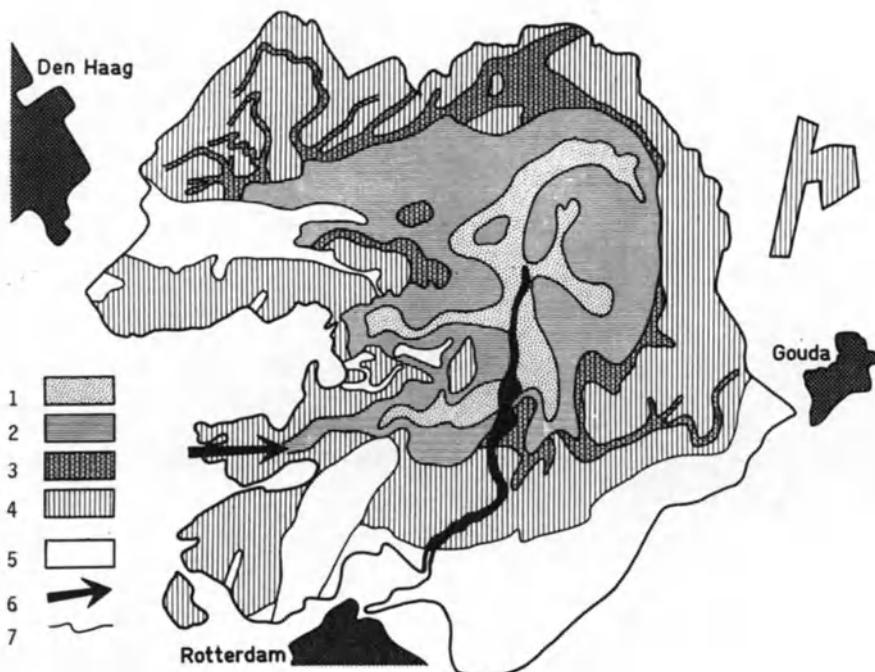
Figure 28.6: Scheme of the lithologic succession in the marine and perimarine area of the Dutch coast



Source: Pons, Jelgersma, Wiggers and de Jong (1963), and Bijlsma (1982)

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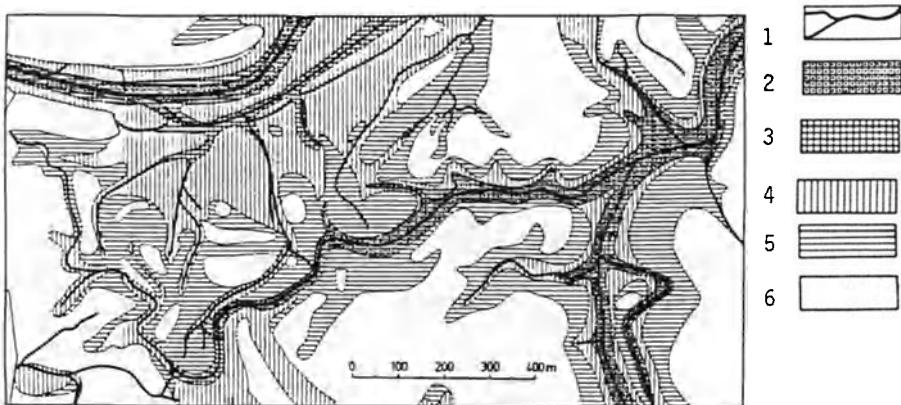
Figure 28.7: The Calais IV a-phase (Wieringermeer-) deposits (surface at about 4 m below present mean sea level) in the central western part of the Netherlands. 1: tidal flat loams; 2: salt marsh clays; 3: brackish reed (*Phragmites*) marsh-clays with broad creek levee-loams and clays; 4: brackish reed marsh-peaty clays; 5: non-cut-over peat lands + older Calais deposits; 6: main entrance of the sea; 7: boundary between deep polders and the non-cut-over peat lands



This sediment unit, termed Calais deposits, IVa-phase, was completed about 5,600 years ago. These tidal flats are clayey, silty, calcareous sands, but along the fringes of these tidal flats are present extensive systems of creeks with calcareous clayey silt levees and highly pyritic, back swamps filled with peaty clays with a reed (*Phragmites*) facies (Figures 28.6 and 28.7).

The peaty clays of the reed facies (brackish conditions) (Figure 28.8) are comparable to the peaty clays of the Rhizophora facies. Both sediments aggraded slowly and vertically and have lower-lying levels of sedimentation, high supplies of organic matter from roots in the reduced soil, and direct tidal influence. The clays of the reed facies show high contents of pyrite and, when empoldered and drained, develop into Sulfaquepts. As in other areas, the physical maturation is poor (Pons, in preparation) and

Figure 28.8: Soil map of a part of the Eendrachtspolder, north of Rotterdam. 1: creek bottoms; 2: calcareous loam; 3: calcareous loam, shallowly overlain by non-calcareous clays (1-2-3: Haplaquepts); 4: non-calcareous clays (Sulfic Haplaquepts); 5: non-calcareous peaty pyritic clays (Sulfaquents and Sulfaquepts)



Source: Edelman (1950)

the soils are not only acid, but show low bearing capacities, low permeability and poor drainage.

Younger sediment units, especially members of the so-called Duinkerken deposits which formed between now and about 3,000 years ago are low in sulfidic materials. This is because of faster and more lateral sedimentation patterns when reed marshes shifted rapidly into newly formed polder land, protected from inundation with saline or brackish water. This faster sedimentation is considered a result of reclamations of forest in the Rhine and Meuse river basins, and the increasing erosion during historical times.

VIETNAM

In South Vietnam, in the Mekong delta, enormous areas of sulfidic muds and acid sulfate soils occur (Moermann, 1961). Recent soil surveys in the southwestern part of the Mekong delta have provided increased knowledge about the occurrences of sulfate acidity. Sulfidic mud distribution and stratigraphy seem to be more and more in accordance with that of the aforementioned potentially acid mud areas in West Africa, South America and in the Netherlands.

Far upstream, in the north-western part of the Mekong river delta between Long Xuyen and Rach Gia, a well-developed, sandy, beach barrier rich in shells was found (Figure 28.9), which was dated as 5,500 years old (Brinkman, Bao ve, Tinh, Phoc Hau and van Mensvoort, in preparation). This remarkable age represents

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the coastline at the end of the Holocene rise in sea level. The sulfidic, peaty clays and clayey peats (2 and 3 of Figure 28.9), north of this ancient coast line were formed prior to 5,500 BP, representing the last part of sedimentation under a rising sea level and environmental conditions comparable to their contemporarily 'vertically' built-up counterparts in Guinea-Bissau, Guiana, and the Netherlands.

Because of the poor drainage, these pyritic clayey peats and peaty clays have formed shallowly developed, very acid ASSoils (Mensvoort and Tri, in preparation).

After 5,500 BP, at about the same sea level the enormous area of the younger delta southeast of the ancient coast (Figure 28.9), has built up rapidly. Brinkman et al. (in preparation) describes the area as a typical 'laterally' formed sediment platform of non-acid alluvial material (NAAM), on top of which locally extensive, but rather shallow (1-2 m) sulfidic materials have formed. Along the main rivers, which seem to have broken only very recently through the acid materials in several places, narrow fluviatile natural levees have formed, wedging out over the sulfidic materials (5, Figure 28.9). Reaching the sea, these clays change into marine clays and contribute to a very rapid lateral extension of the coast. In the somewhat older central parts of the western plain, well-developed Tropaquepts are found as well as Sulfaquepts and Humic Sulfaquepts. The youngest southwestern part of this plain shows Hydraqents, and Sulfaquents, both partly Salic (1, Figure 28.9).

So far, little structure in the geographical distribution of the younger plain, nor subdivision into sediment phases has been noticed.

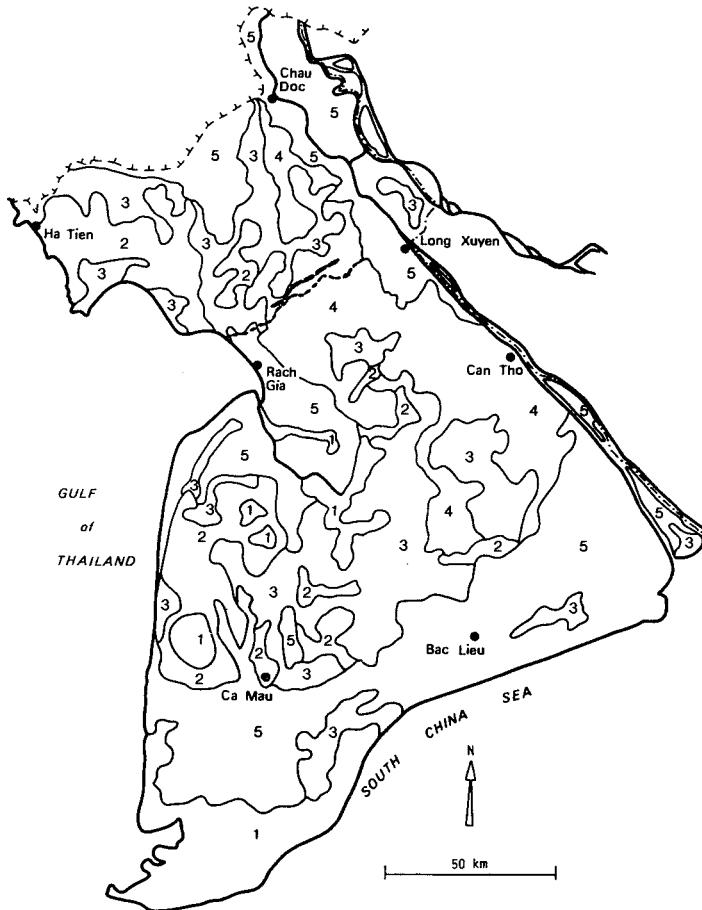
GENERAL CONCLUSIONS

These four sedimentary coastal areas show many similar characteristics, but at the same time are very different in a number of aspects. Tables 28.1 and 28.2 compare some of these aspects. Characteristics and aspects that are equal in at least two contemporaneous sediment units have been underlined.

Interesting conclusions may be drawn from these two tables. Up to 5,500 BP, the sea level rose and this enabled extensive marine and estuarine plains to be formed with very sulfidic clays. These clays were laid down in Rhizophora facies in tropical climates, Phragmites facies under temperature brackish conditions and 'lower-lying mangroves' facies in tropical East Asia. The drainage, soil development and landscapes were greatly influenced by the later movements of sea level.

Generally, with important exceptions in places, after 5,500 BP lateral aggradations prevailed in the coastal areas where sufficient sediment was available to rapidly fill the empty spaces created. In these cases the clays were deposited under an Avicennia or comparable facies (saltmarshes in temperate areas and 'higher-lying mangroves' in east Asia). The sedimentation rate was rapid in all areas resulting in sediments with common low sulfide contents.

Figure 28.9: Provisional soil sketch of the western part of the Mekong delta (southern Vietnam). 1: Sulfaquents; 2 and 3: Sulfaquepts; 4: Sulfic Tropaquepts; 5: Tropaquepts on marine and fluviatile sediments



The soils may be divided into two main groups: the acid sulfate soils (ASS) and the non-acid marine soils (NAMS).

Young acid sulfate soils may be classified as Sulfaquents, Salic Sulfaquents and Sulfihemists. They are not suited for most kinds of agriculture, with the exception of wet-rice cultivation under certain restrictions. The non-sulfidic materials show rapid developments (ripening) which leads from Hydraqents or Salic Hydraqents, via Aeris Hydraqents to Haplaquepts (in temperate areas), or to Tropaquepts and Humaquepts in the tropics. If properly empoldered and drained they are highly productive soils for nearly all types of agricultural land utilization. Older acid sulfate soils are included in the Sulfaquepts and Sulfic

Table 28.1: A comparison of temporaneous sediment-units in coastal Guinea-Bissau and along the Guiana coast: physiography, sea level, facies, clay minerals, potential acidity and soils

Area	Guinea-Bissau	Guiana coast
Climate		trop. hum. - monsoon
>5,500 BP	Luisse deposits	Mara deposits
Sea level	rising to a maximum	rising to present level
Facies	Rhizophora-facies	Rhizophora-facies
Rate of sed.	slow, vertical	slow, vertical
Kind of sed. and potent. acidity	highly sulfidic, kaolinitic clays (to peaty clays); very low neutr. capacity	highly sulfidic, illitic clays to clayey peat; low neutr. capacity
Landscape	estuarine terrace	flat estuarine plain
Drainage (wet s.)	rather well to poorly drained	undr. covered by peat
Soils	Rhodic Sulfaquepts to Rhodic Sulfic Humaquepts	Histic Sulfaquepts
<5,500 BP	Nâabalanta deposits	Coronie deposits
4,000–2,000 BP	Nhala-phase sediments	Wanica-phase sediments
Sea level	slowly rising after drop	constant
Facies	Clays with Rhizophora facies	Clays with Avicennia facies
Rate of sed.	slow vertical	rapidly, lateral
Kind of Sed. and pot. acidity	highly sulfidic clays	clays, low in sulfides
Landscape	very low neutr. cap.	low to med. neutr. cap.
Drainage (wet s.)	flat estuarine plain	flat marine plain
Soils	poorly drained	fairly well drained
	Typic and Salic Sulfaquepts	Tropaquepts
2,000–1,000 BP	?	Moleson-phase sediments
		Avicennia-facies
		item as Wanica-phase

Table 28.1 (continued)

<1,000 (500) BP	Enxudé-phase sediments	Commonine-phase sediments
Facies	Avicennia facies	Avicennia facies
Rate of sed.	rapid lateral sed.	rapid lateral sed.
Kind of sed.	clays, low in sulfides	clays, low in sulfides
Pot. acidity	low to med. neutr. cap.	low to med. neutr. cap.
Drainage	poor to undrained	poor to undrained
Soils	Salic Hydraqents	Salic Hydraqents
	Sometimes: peaty clays of Rh. facies, highly sulfidic: Salic Sulfaqents	

Table 28.2: A comparison of temporaneous sediment-units in the coastal plain of The Netherlands and in the Mekong Delta: physiography, sea level, facies, kinds of sediments, potential acidity, soils

Area	Coastal Netherlands	Western Mekong Delta
Climate >5,500 BP Sea level Facies	temperate humid Calais deposits (Iva sediments) rapidly rising reed (<i>Phragmites</i>) facies, clay + clay loams, illitic slow to rapid, vertical non carbonatic, illite, sulfidic deep drained polders partly well drained, partly covered by peat and water <u>Sulfaquepts, Sulfaquepts and</u> <u>Haplaquepts</u>	monsoon - tropical humid 'older delta' deposits rising to present level 'low-lying mangrove' facies peaty clay to clay peats very slow, vertical sulfidic, illite to smectite flat estuary plain very poor, poor to well drained in dry season <u>Sulfaquepts, Sulfihemists and</u> <u>Sulfaquepts</u>
Rate of sed. Kind of sed. Landscape Drainage (wet s.)		'younger delta' deposits ? constant 'high- and low-lying' mangrove facies
Soils	Duinkerken deposits several sediment units (phases) rising reed (Phr.) to saltmarsh facies	rapid, lateral high to low sulfide contents illitic to smectitic clays flat marine plain poor to rather well in dry well drained <u>Haplaquepts (calc.)</u>
<5,500 BP 4,000-2,000 BP Sea level Facies		Increasing speed of sedimentation, decreasing acidity <u>Haplaquepts</u>
Rate of sed. Kind of sed. Potent. acidity Landscape Drainage Soils		Increasing speed of sedimentation, decreasing acidity <u>Tropaquepts</u>
Younger sediments <2,000 BP		

Tropaquepts, Humaquepts and Haplaquepts. They are poor soils, suited only for certain agricultural activities, and require special, usually difficult and not very economic treatments, e.g. liming, special application of fertilizers, drainage and irrigation manipulations.

On both the younger and the older acid sulfate soils, alternative land use types such as forestry (mangrove or other adapted trees, e.g. Melaleuca, Casuarina, etc.) or nature conservation are much more appropriate.

SUMMARY

Important parts of coastal plain and estuarine wetlands contain sediments with high sulfide contents and the resulting acid sulfate soils.

Four examples of coastal plain deposits are discussed and the occurrences and distributions of the sulfidic muds are described and their origin explained. In the estuaries of Guinea-Bissau and the Mekong delta all deposits from before 5,500 BP were sulfidic and most of those after 5,500 BP also. The Guiana coastal plain shows a sharp break at about 5,500 BP, before which only sulfidic materials were formed and since which only non-sulfidic materials originated. Certain places in the Dutch coastal plain also include extensive areas of the old deposits containing sulfidic materials, whereas the younger deposits are poor in sulfide. In all four areas the subrecent sediments are not potentially acid. The suitability of the different soils for agriculture and for alternative land uses such as forestry, wildlife, nature conservation is discussed.

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Chapter Twenty-nine

SOIL NITROGEN, PHOSPHORUS AND ORGANIC CARBON IN TRANSPLANTED ESTUARINE MARSHES

C.B. Craft, S.W. Broome and E.D. Seneca

INTRODUCTION

Tidal marsh soils serve as sinks in the global carbon cycle (Armentano, 1980) and as reservoirs of organic materials for estuarine ecosystems (Friedman and DeWitt, 1978). Although marshes and other wetlands encompass less than 2 per cent of the world's land surface, they contain about 10 per cent of the total terrestrial soil organic carbon (Schlesinger, 1977). The high net primary production (NPP) and water-saturated conditions result in rapid accumulation of organic materials in marsh soils.

In recent years, estuarine marsh vegetation has been established to stabilize dredged material, reduce shoreline erosion and mitigate damage to wetlands related to surface mining (Woodhouse, Seneca and Broome, 1974; Broome, Seneca and Woodhouse, 1986). These transplanted marshes develop a continuous cover with NPP comparable to adjacent natural marshes within a few years of establishment. However, the role of transplanted marshes as estuarine nutrients reservoirs has not been investigated.

The objectives of this study were to assess N, P and organic C pools in transplanted and adjacent natural marsh soils. Total N, P and organic C were measured in soil and macro-organic matter (>2 mm fraction). Rates of soil organic matter accumulation in a natural and a transplanted marsh were estimated.

METHODS

Soils and macro-organic matter (MOM) were sampled at five sites along the North Carolina coast during the summer of 1984. Each site consisted of a natural and an adjacent transplanted marsh. The transplanted marshes were established within the past 15 years; Oregon inlet (1969), Snow's Cut (1970), Pine Knoll Shores (1974), Texasgulf (1980) and NC Phosphate (1983). Three locations, Oregon inlet (OI), Snow's Cut (SC) and Pine Knoll Shores (PK), were regularly flooded marshes dominated by Spartina alterniflora. The other two sites, Texasgulf (TG) and NC Phosphate (NC) were irregularly flooded marshes colonised by Spartina spp., Juncus roemerianus, Distichlis spicata and Cladium jamaicense.

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Soil and MOM were sampled using a corer, 8.5 cm diameter by 30 cm deep. Between 10 and 20 soil cores were randomly collected from each marsh (Craft, Broome and Seneca, 1986). Soil cores were air-dried, weighed, ground and passed through a 2 mm sieve. Macro-organic matter was sampled by collecting a second core from each sampling point. Cores were washed on a 2 mm screen and the organic material retained was dried at 70°C for 48 hours, weighed and ground.

Soil and MOM were analyzed for total N, P and organic C. Organic matter was measured by loss on ignition at 450°C and converted into organic C by multiplying by 0.45. Total N (organic + NH₄-N) was determined by Kjeldahl digestion (Bremner and Mulvaney, 1982). Total P was measured using perchloric acid digests (Sommers and Nelson, 1972). Elemental concentrations were expressed on a dry weight (105°C) basis. Soil bulk density was estimated by weighing the air-dried cores and applying a moisture correction factor determined during loss on ignition.

RESULTS AND DISCUSSION

Dry weight of MOM was much lower in transplanted than natural marshes (Table 29.1). Macro-organic matter increased as transplanted marshes developed and, at one site, approximated the adjacent natural marsh 14 years after establishment. Dry weight of MOM was also dependent on hydrology. With the exception of Oregon inlet, irregularly flooded natural marshes contained the largest amounts of MOM.

There was no difference in carbon content of MOM collected from natural and planted marshes (Table 29.1). However, irregularly flooded marshes had higher MOM carbon levels than regularly flooded marshes. Irregularly flooded marshes are colonized by Juncus, Cladium and S. patens which have higher tissue C than S. alterniflora (Craft et al., 1986), the dominant macrophyte in regularly flooded salt marshes. Macro-organic matter N concentrations were much higher in natural marshes (Table 29.1) and probably resulted from a greater proportion of decaying roots in these older marsh soils. Percentage nitrogen in marsh vegetation generally increases during decomposition (Hackney and Cruz, 1980) as plant N is converted into microbial tissue (Cruz, 1975). In contrast to N, phosphorus content of MOM was greater in transplanted marshes. Again, the relative proportion of live below ground material may account for this difference as living roots and rhizomes have higher P than decaying material (Cruz and Hackney, 1977).

Soil organic matter was lower in transplanted than adjacent natural marshes, resulting in higher bulk densities and less total N, P and organic C (Table 29.2). Soil C and N were greatest in the irregularly flooded natural marshes. Organic matter accumulation in estuarine marshes generally increases with decreasing frequency of flooding (Gosselink and Turner, 1978). In irregularly flooded marshes, most NPP accumulates on the marsh and only a small amount is removed by tides (Hackney and Cruz, 1982).

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Table 29.1: Mean dry weight, carbon (C), nitrogen (N) and phosphorus (P) of macro-organic matter collected from natural and planted marshes

Marsh	Site	Dry weight (g m ⁻²)	C (mol kg ⁻¹)	N (mmol kg ⁻¹)	P
Natural	OI	5330±672 ^a	31.8±0.52	520±28	15±3.3
	SC	3460±266	33.0±0.36	510±17	17±1.1
	PK	2790±205	32.1±0.79	580±21	25±1.4
	TG	6440±426	34.8±0.28	530±11	13±1.3
	NC	4920±509	35.0±0.22	650±20	14±1.1
Planted	OI (15) ^b	2350±149	32.4±0.92	460±32	19±3.4
	SC (14)	3026±338	32.5±0.39	460±15	19±1.5
	PK (10)	1660±171	32.3±0.45	430±16	17±0.9
	TG (4)	1240±185	33.6±0.39	460±23	25±2.0
	NC (1)	220±30	-	410±34	21±1.2

Notes: a, Standard error of the mean.

b, Age of transplanted marsh.

c, Insufficient MOM to perform this analysis

Table 29.2: Mean bulk density, carbon (C), nitrogen (N) and phosphorus (P) of natural and planted marsh soils

Marsh	Site	Bulk density (Mg m ⁻³)	C (mol kg ⁻¹)	N (mmol kg ⁻¹)	P
Natural	OI	1.3±0.03 ^a	1.1±0.18	60±11	4±0.4
	SC	0.4±0.02	8.3±0.50	340±21	16±0.6
	PK	1.3±0.04	0.3±0.02	20± 1	17±0.6
	TG	0.2±0.02	17.7±1.28	950±68	24±1.2
	NC	0.2±0.02	18.7±1.01	1100±61	30±1.7
Planted	OI (15) ^b	1.3±0.04	0.3±0.06	30± 5	2±0.2
	SC (14)	1.1±0.02	0.8±0.05	30± 2	4±0.3
	PK (10)	1.4±0.02	0.3±0.02	10± 1	14±0.7
	TG (4)	1.3±0.03	1.6±0.07	50± 2	3±0.1
	NC (1)	1.1±0.05	0.4±0.02	10± 1	3±0.3

Notes: a, Standard error of the mean.

b, Age of transplanted marsh.

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Table 29.3: Carbon, nitrogen and phosphorus pools (kmol ha^{-1}) in the top 30 cm of natural and planted marshes

Marsh	Site	Carbon		Nitrogen		Phosphorus	
		Soil	MOM	Soil	MOM	Soil	MOM
Natural	OI	3517	1688	203	26	14.0	0.7
	SC	8898	1141	364	18	17.3	0.6
	PK	1110	898	56	16	61.5	0.7
	TG	9443	2231	505	34	13.1	0.8
	NC	7067	1733	415	31	11.8	0.6
Planted	OI (15) ^a	924	760	75	11	5.7	0.4
	SC (14)	2040	980	75	14	12.3	0.6
	PK (10)	1002	537	43	7	57.8	0.3
	TG (4)	6234	409	119	6	11.0	0.3
	NC (1)	1307	-	44	1	10.6	0.1

Note: a, Age of transplanted marsh.

Soil P increased with increasing organic matter content; the greatest concentrations were in the irregularly flooded natural marshes. The only exceptions to this trend were the two Pine Knoll Shores marshes, which contained little soil organic matter, but had high P levels. These marshes are surrounded by intensive development so septic effluent and fertilizer runoff are believed to contribute significant amounts of P to the marshes.

Carbon and nitrogen pools were much greater in natural than transplanted marshes (Table 29.3). With the exception of the Texasgulf site, which had topsoil applied during establishment, organic matter reservoirs increased with transplanted marsh age. The 14- and 15-year old marshes contained the most N and organic C whereas the 1-year-old marsh contained the least. Phosphorus pools were less dependent on soil organic matter than C and N and were greatest in the Pine Knoll Shores marshes. Most C, N and P was present in the soil fraction with MOM contributing 6-45 per cent, 2-22 per cent and 0-7 per cent to the C, N and P pools respectively.

Rates of soil organic C accumulation (1979-1984) were calculated for the Pine Knoll Shores marshes using the data of Broome et al., (1986). Organic C accumulation (top 30 cm) was similar in the natural ($18.7 \text{ mol m}^{-2} \text{ yr}^{-1}$) and transplanted ($18.9 \text{ mol m}^{-2} \text{ yr}^{-1}$) marsh. Fifty-four per cent (10.2 mol) of the C was buried in the upper 10 cm of the transplanted marsh compared to 33 per cent (6.2 mol) in the natural marsh. Estimates of above and below ground NPP in the natural ($58.0 \text{ mol m}^{-2} \text{ yr}^{-1}$) and transplanted ($61.9 \text{ mol m}^{-2} \text{ yr}^{-1}$) marsh (Broome et al., 1986) indicated that 31-32 per cent was buried in marsh sediments each year.

In conclusion, transplanted marshes are early successional communities which may serve as nutrient reservoirs for estuaries.

While MOM nutrient pools develop rapidly (15-30 years) in transplanted marshes, soil C, N and P pools take considerably longer.

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PART V

THE TOLERANCE OF PLANT SPECIES TO WETLAND SITES

Chapter Thirty

BIOCHEMICAL ADAPTATIONS TO ANOXIA IN BARNYARD GRASS

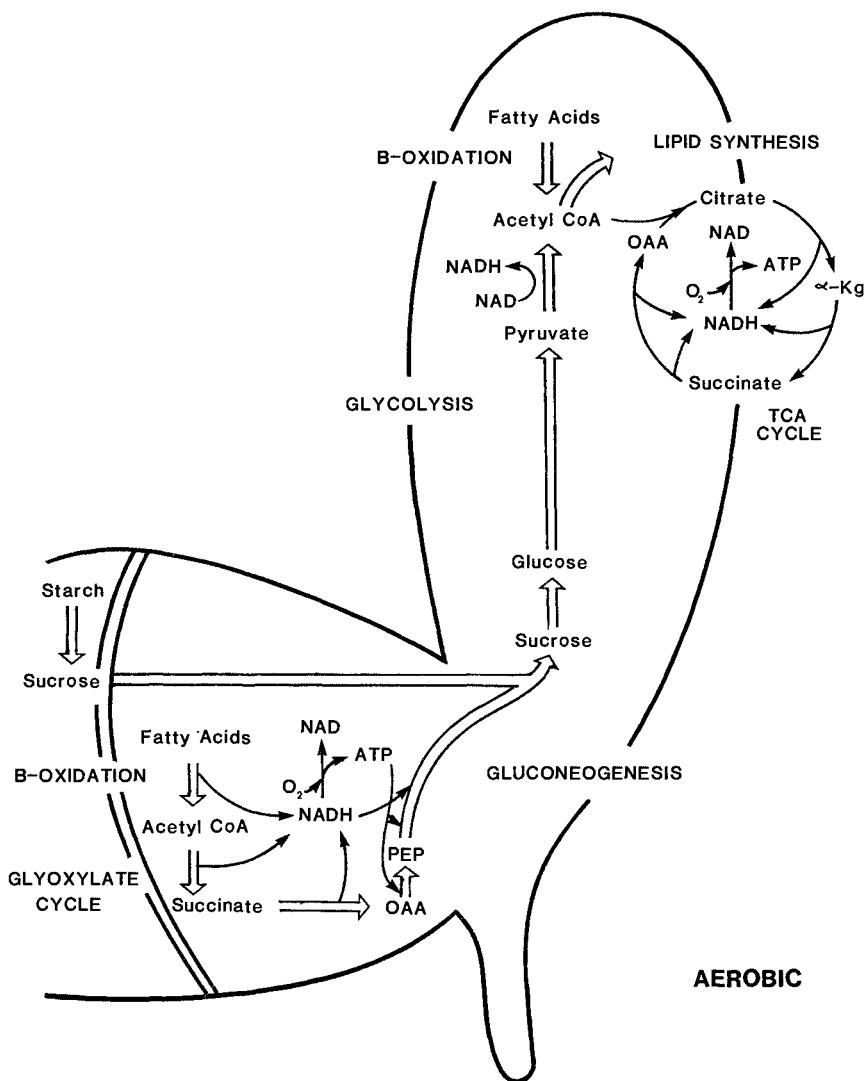
Theodore C. Fox, Robert A. Kennedy and Ali A. Alani

Although higher plants require oxygen for growth, they frequently experience low oxygen environments which occur in natural wetlands and during flooding or irrigation. Plants tolerate these conditions for only a short period of time before irreversible damage occurs. We have been studying a group of rice weeds which, like cultivated rice (*Oryza sativa*), can germinate and grow without oxygen. *Echinochloa crus-galli* var. *oryzicola* (hereafter *oryzicola*) metabolizes its seed reserves under N_2 and produces a larger seedling from a smaller seed than rice (Kennedy, Rumpho and VanderZee, 1983b). In response to temperature, *oryzicola* and rice exhibit similar germination characteristics under aerobic conditions. Under anaerobic conditions, however, *oryzicola* germinates better and tolerates colder temperatures than rice. Thus, both *Echinochloa* and rice provide excellent opportunities to study metabolic adaptations to low oxygen stress. In addition, the *Echinochloa* 'complex' is composed of several species that differ in their ability to germinate under anoxia (Kennedy et al., 1983b), each exhibiting a full range of habitat preference and weediness in rice cultivation - an ideal natural system for comparative studies on the biochemistry of these important weed species.

The main carbohydrate reserve in seeds of cereals and other Graminaceous plants is starch (Bewley and Black, 1978). This is also true in *oryzicola*. Our studies indicate that oxidation of storage products within the seed (principally carbohydrate) provides the carbon and energy required for germination and initial seedling growth. Under aerobic conditions, oxygen serves as the primary electron acceptor and permits full operation of the conventional metabolic cycles (Figure 30.1). Degradation of starch to glucose-6-phosphate, which may enter either the glycolytic or oxidative pentose phosphate (OPP) pathway, or to sucrose is an important first step in the utilization of carbon reserves during germination. Lipids, which comprise 5 per cent of the seed dry weight in *oryzicola*, are metabolised to sucrose by β -oxidation, the glyoxylate cycle and subsequently gluconeogenesis. Sucrose is translocated to the root and shoot where it is metabolized via glycolysis and the TCA cycle. Lipid deposits in the shoot are also metabolized by β -oxidation to acetyl CoA which enters the TCA cycle.

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Figure 30.1: Major flow of carbon in seeds of Echinochloa crus-galli var. oryzicola germinated in air



In the absence of oxygen, most metabolic pathways are thought to be greatly reduced or to cease functioning altogether for lack of an appropriate electron acceptor or adequate supplies of oxidized coenzymes. Glycolysis is an exception. Our studies of oryzicola indicate quite the opposite; anaerobic metabolism in oryzicola is a comprehensive and highly coordinated process (Figure 30.2). Whereas fermentation appears to be the predominant feature of anaerobic metabolism in oryzicola (Rumpho and Kennedy, 1981; Rumpho and Kennedy, 1983a), the OPP pathway is operative during anaerobic germination. Furthermore, lipid metabolism and the TCA cycle also function under anoxia.

Here, we will examine the contributions of several key metabolic pathways to the overall metabolism of oryzicola during anaerobiosis, making comparisons with other Echinochloa species and rice.

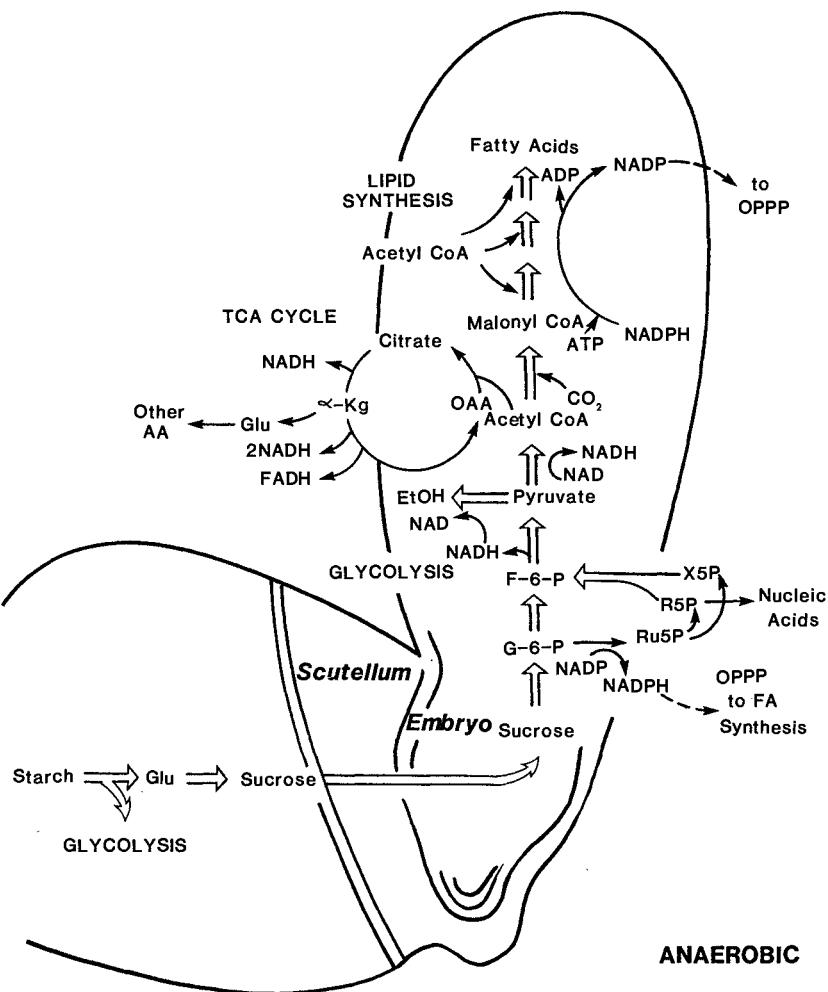
FERMENTATIVE METABOLISM

Under anaerobic conditions, formation of ATP is thought to be dependent on substrate level phosphorylation from glycolysis (Pradet and Bomsel, 1978). One measure of the efficiency of this process is the adenylate energy charge (AEC). In seeds germinated in air, AEC values typically range from 0.8 to 0.9. Upon transfer to anoxic conditions, AEC generally declines to 0.2 to 0.5 in seeds with predominantly fat reserves and to 0.5 to 0.8 in seeds with predominately starch reserves (Raymond, Alani and Pradet, 1985). Among several Echinochloa species grown in N₂ for 7 days, AEC values were high and there was little difference among the species; AEC values ranged from 0.7 to 0.9. The species tested did separate into two distinct groups, however, based on their total adenylate content. E. crus-galli var. crus-galli and E. crus-pavonis exhibited little ability to synthesize adenylates during anoxia, whereas oryzicola, E. muricata and rice exhibited linear increases of adenylates with time under anoxia (Kennedy, Rumpho and Fox, 1986). The species that were unable to synthesize adenylates are intolerant of flooding, whereas the species that readily synthesized adenylates are very flood tolerant. The ability to synthesize adenylates, as opposed to AEC, may be an important indicator of flood tolerance among Echinochloa species.

We have found that alcohol dehydrogenase (ADH) activity and ethanol production are high in anaerobically germinated seeds of oryzicola, whereas malate, lactate, or other organic acids do not accumulate significantly (Rumpho and Kennedy, 1983). High ADH activity permits increased glycolysis and ATP formation via substrate level phosphorylation. The reasons why some plants or tissues are killed under anoxia is unknown, but alcohol and acetaldehyde toxicity and acidosis have been implicated (Garlic, Radda and Seeley, 1979; Bore, Sehr, Chan, Thulborn, Ross and Radda, 1981; Roberts, 1985). In oryzicola, alcoholic fermentation appears to be maintained by its ability to vent most of the ethanol produced to the external medium (Rumpho and Kennedy, 1981), its ability to metabolize at least some of the remaining alcohol (Rumpho

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Figure 30.2: Major flow of carbon in seeds of Echinochloa crus-galli var. oryzicola germinated in N_2



and Kennedy, 1981, 1983a), and by possessing a high inherent tolerance to increasing ethanol concentrations (Rumpho and Kennedy, 1983a).

An important aspect of *oryzicola*'s adaptation to anaerobic growth appears to be its ADH isoenzyme pattern. In an effort to understand the relationship between ADH isoenzymes and flood tolerance, we examined the ADH isoenzyme complement of several *Echinochloa* species. The number of isoenzymes varied greatly and bore no correlation with the ability of the species to tolerate flooding (Kennedy et al., 1986).

Although the number of ADH isoenzymes may not be important to withstanding low oxygen, induction of ADH isoenzymes might be. We have found that *oryzicola* exhibits three ADH isoenzyme bands in dry, unimbibed seeds, but four isoenzymes in seeds germinated in N₂ (Kennedy et al., 1986). In air-germinated seeds, the fourth isoenzyme is not present, but may be induced in the presence of ethanol. Thus, the induction of ADH isoenzymes may be important in *oryzicola* to tolerate high ethanol concentrations by allowing for increased ethanol metabolism.

Localization of ADH activity within the plant also appears to be an important determinant of flood tolerance. Flood-tolerant species such as *oryzicola* and rice have approximately two thirds of their total ADH activity located in the shoot, whereas unadapted species, such as corn and pea, have approximately two-thirds of their total ADH activity in the roots (Cobb and Kennedy, 1987). This localisation of ADH within the seedling could be an extremely important adaptation to flood tolerance. In a flooded environment, the soil/water interface is totally anaerobic (Chapman and Mikkelsen, 1963; Barclay and Crawford, 1982). Under such conditions, it would be energetically advantageous for seeds to allocate most of their reserves, via fermentative metabolism, into producing a shoot that might elongate and enter a more aerobic zone. Conversely, the most deleterious strategy would be to expend energy on the roots at the expense of the shoot. Our findings are not surprising since flood-tolerant plants have long-been recognized to have reduced root growth under anaerobic conditions whereas shoot growth is stimulated (Taylor, 1942; Kennedy, Barrett, VanderZee and Rumpho, 1980; Kordon, 1974)

OXIDATIVE PENTOSE PHOSPHATE PATHWAY

Although glycolysis supplies most of the energy and NADH necessary for germination (apRees, 1980), the OPP pathway is an important supplier of certain metabolic intermediates and of NADPH for fatty acid synthesis (Pryke and apRees, 1976; Purvis and Fites, 1979). The OPP pathway provides pentose monophosphates which are essential for the biosynthesis of nucleotides and RNA. Furthermore, synthesis of fatty acids is required for lipid synthesis and membrane formation during the germination process. Under anoxic conditions, when the OPP pathway might be expected to cease functioning for lack of oxidized coenzymes, lipid synthesis could also serve to regenerate NADP⁺, thereby permitting continued OPP pathway operation.

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We have investigated the contribution of the OPP pathway to the overall metabolism of oryzicola seedlings grown in air and nitrogen through studies of key glycolytic and OPP pathway enzymes. Our enzymatic studies indicate that fructose-1,6-bisphosphate aldolase, not phosphofructokinase, was more important in regulating glycolytic activity in oryzicola (Rumpho and Kennedy, 1983b). Glucose-6-phosphate dehydrogenase, a key regulatory enzyme of the OPP pathway, was present at similar activities in both aerobically and anaerobically grown seedlings during the first three days of germination; thereafter, activity in air-grown seedlings increased, whereas that in N_2 -grown seedlings remained constant. Comparison of the ratio of the activities of aldolase and glucose-6-phosphate dehydrogenase at several times during seed germination indicated that the relative importance of glycolysis and the OPP pathway in aerobically and anaerobically germinated seedlings were similar for three days. Subsequently in air, the ratio shifted suggesting that the OPP pathway gained in importance compared to the glycolytic pathway. In N_2 grown seedlings, the converse pattern was observed.

Further evidence that the OPP pathway operates during anaerobiosis comes from metabolism of specifically labelled [^{14}C] glucose by oryzicola (Kennedy et al., 1983b; Rumpho and Kennedy, 1983b). In air-grown seedlings, malate and fumarate were heavily labeled, whereas in anaerobically germinated seedlings, phosphorylated sugars and lipids were predominantly labeled. In oryzicola seedlings grown in air, metabolism of [$1-^{14}C$] glucose resulted in a greater percentage of label in CO_2 , while metabolism of [$6-^{14}C$] glucose resulted in a greater percentage of label in ethanol. In anaerobically grown seedlings, these differences were more pronounced, particularly during the first 24 hours of germination. These results suggest that at least in oryzicola, OPP pathway activity increases under N_2 .

LIPID METABOLISM

One of the most striking ultrastructural features of oryzicola and rice grown under N_2 is an accumulation of lipids (spherosomes). This accumulation occurs in an acropetal direction and a 'front' of lipid deposition appears to move up the meristem. We have verified this increase of lipids by quantitative analysis (Knowles and Kennedy, 1984; Everard and Kennedy, 1985) and by uptake and metabolism of ^{14}C -labeled substrates (acetate, sucrose, glycerol), followed by autoradiography (Everard and Kennedy, 1985). Furthermore, initial electron-microscopy experiments indicate that the lipid that accumulates under N_2 disappears if the seedlings are subsequently grown in air. These observations are of particular importance for several reasons. First, if lipid synthesis occurs without oxygen, it would serve to reoxidize NADPH produced by the OPP pathway. We know that the OPP pathway operates under N_2 and such a mechanism would permit continued metabolic cycling of carbohydrate metabolism that would otherwise stop for lack of NADP. Second, lipid synthesis would be needed directly for the formation and stabilization of membranes. Our electron-microscopic

studies show conclusively that a large degree of membrane synthesis occurs even without oxygen (VanderZee and Kennedy, 1982). Third, accumulation of lipid would serve to store important carbon skeletons for subsequent use under aerobic conditions.

In support of this hypothesis, we have found that fatty acids are synthesized in oryzicola in the complete absence of O₂ (Everard and Kennedy, 1985) and that a surprising amount of unsaturated fatty acids remain during germination (Knowles and Kennedy, 1984), thereby preserving membrane integrity even during anaerobiosis. Preliminary evidence indicates that lipid accumulation in primary leaves results from the carboxylation of acetyl CoA derived from carbohydrate. Activity of acetyl CoA carboxylase in anaerobic seedlings was similar to that in aerobic tissue.

Recently, we have begun to use mass spectrometry to determine the natural abundance of carbon isotopes in oryzicola seedlings. Determination of the stable carbon isotope ratio (¹³C/¹²C) allows identification of the carbon source when several substrates are respired. In preliminary experiments (Table 30.1), we were able to determine that aerobic seedlings use lipids as a major respiratory substrate during the first four days of germination, shifting towards increased carbohydrate oxidation for the next ten days. Anaerobic seeds, on the other hand, primarily metabolize carbohydrates at all time periods surveyed. Recent enzyme data for lipid metabolism confirm these results; air-grown seeds had high isocitrate lyase activity, an indication of glyoxylate cycle operation, whereas anaerobically grown seedlings did not. In addition, when seedlings were transferred from N₂ to air, isocitrate lyase activity increased in seeds, but not in shoots. That is, the seed proper has the capability to metabolize lipid via the glyoxylate cycle, whereas the shoot does not. These results support our hypothesis that lipid synthesis and accumulation under anoxia may function for the reoxidation of NADPH, rather than serving as an immediate energy source. Subsequently, oxidation of fatty acids via β -oxidation may serve as a potent energy source under aerobic conditions.

MITOCHONDRIAL METABOLISM

In spite of the central role of mitochondria in aerobic metabolism, very little is known about their role under anoxia. In general, mitochondria have been assumed to be inoperative in higher plants during anaerobiosis since they would cease to function for lack of oxidized coenzymes and a terminal electron acceptor, i.e. molecular oxygen. In support of this, flood-intolerant species, and even flood-tolerant species such as rice, develop ultrastructurally abnormal mitochondria when exposed to anoxia (Ueda and Tsuji, 1971; Oliveira, 1977; Vartepetian, Andreera, Kozlova and Agapova, 1977). In oryzicola, on the other hand, the ultrastructure of mitochondria in anaerobically grown seedlings is indistinguishable from that of seedlings grown in air (Kennedy *et al.*, 1980). This observation led us to suspect that in oryzicola, mitochondria may indeed function to some extent, even during anaerobiosis.

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Table 30.1: Carbon isotope ratio of CO₂ respired from Echinochloa crus-galli var. oryzicola seedlings germinated under aerobic or anaerobic conditions. In general, lipid reserves are more depleted (more negative) in ¹³C than carbohydrates or protein compared to the PDB standard. In spite of a large accumulation of lipid in shoots of oryzicola seeds germinated under N₂, the data below indicates that lipids are respired to a greater extent under aerobic conditions than during anaerobiosis. In both environments, however, there is a shift to the use of carbohydrates with increasing time, i.e. the δ^{13} values become less negative.

Days after imbibition	δ^{13}	
	Aerobic	Anaerobic
2	-	-12.97
3	-24.20	-12.96
4	-23.26	-11.11
13	-18.17	- 8.57

Many invertebrates utilize a partial TCA cycle under anoxic conditions. Hochachka and Mustafa (1972) presented evidence that the part of the TCA cycle catalyzed by citrate synthase, aconitase, isocitrate dehydrogenase, α -ketoglutarate dehydrogenase, and succinyl CoA synthase operates. The possibility that oryzicola may also possess at least partial TCA-cycle activity was evidenced from [¹⁴C]sucrose and [¹⁴C]acetate uptake studies in which TCA-cycle intermediates were formed (Rumpho and Kennedy, 1981). Part of the difficulty in studying these reactions, however, is that all TCA cycle intermediates can be formed by other routes or by partial operation of the TCA cycle in either direction. Recent studies *in vitro* indicate that most TCA-cycle enzymes are operating in oryzicola during anaerobic germination (Table 30.2). The activities of cytochrome c oxidase, isocitrate dehydrogenase, aconitase, succinyl CoA synthase, succinate dehydrogenase, and fumarase in N₂-germinated seeds were 50-80 per cent of the activities in aerobic controls after 5 days germination. In contrast, α -ketoglutarate dehydrogenase activity was only 30 per cent of the controls. Thus, most, if not all, of the TCA cycle operates in oryzicola during anaerobiosis. And perhaps even more striking, most TCA-cycle enzyme activities in anaerobically grown seedlings are remarkably close to those in aerobically grown tissue.

We have found that germination of rice in air is unaffected by the presence of KCN or NaN₃ (Kennedy et al., 1986). Rice apparently shifts to a cyanide-insensitive pathway since cyanide and SHAM (inhibitors of conventional and alternative mitochondrial electron transport chains, respectively) totally inhibited germination when both were included in the medium. In contrast, cyanide or azide inhibited the germination of oryzicola with or without

Table 30.2: Activity of mitochondrial enzymes in seedlings of Echinochloa crus-galli var. oryzicola grown under aerobic or anaerobic conditions for 5 days

Enzyme	Enzyme activity (nmol min ⁻¹ mg ⁻¹ protein)	
	Aerobic	Anaerobic
Cytochrome c oxidase	209.8	149.0
Isocitrate dehydrogenase	57.3	45.6
Aconitase	272.0	167.8
Succinyl CoA synthase	354.4	217.7
α -Ketoglutarate dehydrogenase	166.8	52.5
Succinate dehydrogenase	138.8	78.4
Fumarase	106.4	68.3

the presence of oxygen. SHAM had no affect on anaerobic germination. These results suggested to us (Kennedy et al., 1980; Kennedy et al., 1983b) that oryzicola may use a terminal electron acceptor other than O₂ when germinated under anaerobic conditions. Reduction of an alternative electron acceptor, such as nitrate (Gambrell and Patrick, 1978), organic acids (Hochachka, 1980; Gade, 1983) or lipids (as discussed above) could permit electron transport in the absence of oxygen. In support of this hypothesis, we have found that nitrate reserves are depleted during germination (Kennedy et al., 1983b). However, lack of an inhibitory effect of CO, a more-specific inhibitor of cytochrome c oxidase, suggests that regardless of the effect(s) of cyanide and azide, it is not through cytochrome c oxidase. Whatever the mechanism, we know that oryzicola differs from rice in its response to metabolic inhibitors, suggesting that different oxygen-insensitive respiratory mechanisms function in these two organisms.

In extending these studies to other rice weeds, we have found that they differ markedly in their sensitivity to SHAM, KCN, NaN₃, CO, and various combinations of these inhibitors (Kennedy et al., 1986). In the laboratory, we can selectively inhibit all Echinochloa species with no effect on rice, and we can inhibit germination of flood-intolerant species without affecting flood-tolerant ones. These data provide information about differing sensitivity to inhibitors among these species and suggests clues about the possible development of selective herbicides for controlling or eliminating them from agricultural crops.

Currently, we are investigating the activity of mitochondria isolated from oryzicola seedlings grown under air and N₂. Although oxygen uptake was low in N₂-grown seedlings, mitochondrial activity rapidly increased when the seedlings were exposed to air (unpublished data). Mitochondria from both aerobically and anaerobically germinated seeds possessed remarkably good respiratory control and ADP/O ratios, indicating strong control by ADP. Finally, reduced-minus-oxidized absorption spectra revealed not

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only an additional absorption peak in anaerobic mitochondria, but also differences in the reduction of cytochromes due to treatment. Cytochromes b_{565} and $a.a_3$ were more reduced by the treatment under anoxia than they were under air. Cytochrome c was more reduced in air than under nitrogen. Cytochrome b_{577} , on the other hand, was not detectable in aerobic mitochondria, but showed a highly reduced spectrum in anaerobic mitochondria.

Our most recent experiments also suggest that oryzicola differs fundamentally from most higher plants. Oryzicola exhibits an unusually large residual respiration (oxygen uptake remaining after the addition of KCN and SHAM) under both aerobic and anaerobic conditions. Whereas CN^- and SHAM reduce mitochondrial respiration to less than 20 per cent of the control value in most other plant mitochondria (Lance, Chauvean and Dizengremel, 1985), oryzicola retains up to 66 per cent of its initial respiration rate in the presence of these inhibitors. Furthermore, the effects of cyanide and azide are additive, regardless of the order in which the inhibitors are added to the reaction mixture. Antimycin A is also not an effective inhibitor of oxygen uptake in oryzicola mitochondria.

You will note that, while cyanide and azide inhibit germination of Echinochloa seeds, these compounds are surprisingly ineffective in inhibiting the activity of isolated mitochondria. This is not contradictory since these inhibitors affect very different metabolic aspects in the two systems. In whole seeds, the mechanism(s) of inhibition is unknown. However, one of the known effects of cyanide is its inhibition of lipid synthesis (Wareing and Laties, 1977). This is interesting since we are proposing an important role for lipid synthesis in Echinochloa's ability to tolerate anaerobiosis.

Most interesting, we observed an absorption maximum in the cytochrome d region of the reduced-minus-oxidized spectra in both aerobic and anaerobic mitochondria of oryzicola. Cytochrome d has been reported only in bacterial respiratory chains, where it exhibits several interesting functions (Poole, 1983): (a) it serves as a terminal electron acceptor, (b) it is insensitive to cyanide, (c) it has a high affinity for oxygen, (d) its appearance is enhanced by hypoxia and anoxia, (e) it utilizes N-compounds such as nitrite and nitrate as terminal electron acceptors, and (f) it is not involved in energy conservation.

In oryzicola, cytochrome d may function in a similar manner. If so, cytochrome d could account for some of the unusual features of mitochondrial electron transport that we have observed in oryzicola. For instance, cytochrome d provides a third branch in the electron-transport system, in addition to the conventional and alternative pathways, thereby accounting for the large amount of residual respiration. Furthermore, we have found that nitrate reserves in oryzicola seeds are depleted by approximately 75 per cent during the initial 24 hours of germination, consistent with reduction of nitrate by cytochrome d .

In addition to mitochondrial function under anoxia, the ability metabolically to shift from an anaerobic mode to an aerobic one may be an important feature of oryzicola in terms of its weediness in rice fields. Upon transfer from N_2 to air, mitochondria isolated from oryzicola exhibited rapidly increasing rates of oxygen uptake.

Mitochondria isolated from rice coleoptiles, on the other hand, increased respiratory activity only after 30 min in air (Vartapetian, 1978). The lag in respiratory development exhibited by rice may be traceable to specific mitochondrial enzymes. For example, we found that cytochrome *c* oxidase activity in rice seedlings is decreased during the first hour in air, whereas that in oryzicola seedlings remained constant during that period.

PHOTOSYNTHETIC METABOLISM

Following germination, development of photosynthetic competency is essential for seedling establishment. In the absence of oxygen, oryzicola seeds germinate and produce a 2-3 cm unpigmented seedling after seven days of growth. Beyond the initial germination stage, seedlings require oxygen for further development and vigorous growth. If oxygen is then supplied, the shoots green up, chloroplasts develop, and photosynthesis proceeds with only a short lag compared to etiolated seedlings (VanderZee and Kennedy, 1982; Kennedy *et al.*, 1983b).

Under anaerobiosis, plastid size and stroma thylakoid numbers increased markedly in oryzicola (VanderZee and Kennedy, 1982). Plastid morphology is characterized by development of prolamellar bodies, previously reported only in etiolated tissues. Upon transfer to air, seedlings rapidly synthesize chlorophyll, ribulose-1, 5-bisphosphate (RuBP) and phosphoenolpyruvate (PEP) carboxylases, and begin to fix CO₂ (Kennedy, VanderZee and Bozarth, 1983c). Compared to chlorophyll synthesis, however, CO₂ fixation and enzyme activity exhibit a lag. It is curious to note that, when transferred from N₂ to air, the kinetics for the development of CO₂ fixation capability more closely parallels the development of PEP carboxylase activity than it does that of RuBP carboxylase (Kennedy, Bozarth and Hetyei, 1983a). When the seedlings green up under water, however, just the opposite occurs; RuBP carboxylase predominates over PEP carboxylase and more closely parallels the overall CO₂ uptake rate. These results suggest that, as far as development of photosynthesis, anaerobic versus aquatic environments are not alike and the development of components of the photosynthetic apparatus respond differently under the two conditions (Kennedy *et al.*, 1983c).

Compared to rice, photosynthetic activity in oryzicola occurs after a shorter lag time (Bozarth and Kennedy, 1985). Furthermore, once photosynthetic activity begins, maximum photosynthetic rates are achieved more rapidly in oryzicola than in rice. The more rapid development of photosynthesis in oryzicola relative to rice may be another factor contributing to oryzicola's success as a weed species.

CONCLUSION

Our studies on Echinochloa reveal a comprehensive and integrated pattern of anaerobic metabolism. We have evidence that, whereas several conventional metabolic pathways contribute to the overall

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metabolism during anaerobic germination, Echinochloa also has unique fundamental adaptations which may impart tolerance. We have documented both aspects, the comprehensive picture of anaerobic carbon metabolism and the unique adaptations, in previous studies (Kennedy et al., 1983a; Rumpho and Kennedy, 1983b; Knowles and Kennedy, 1984; Kennedy et al., 1986).

In air, the usual catabolic and anabolic reactions lead to starch breakdown, energy generation, and structural and functional features of the cells. During anoxia, Echinochloa retains much of what we have ascribed to 'aerobic respiration'; glycolysis is very active, along with the TCA cycle and the OPP pathway. In addition, our studies show for the first time that anabolic reactions may be as important as catabolic ones. The very active synthesis of lipid in the expanding shoots most likely serves to regenerate NADP, allowing cyclic metabolism to continue. Finally, this specialized carbon metabolism may be complemented by unique electron-transport characteristics. Perhaps the most important aspect of Echinochloa's ability to tolerate anoxia could be in its possession of an unusual cytochrome which would allow it to function energetically in the absence of oxygen.

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Chapter Thirty-one

INVOLVEMENT OF THE HORMONES ETHYLENE AND ABSCISIC ACID IN SOME ADAPTIVE RESPONSES OF PLANTS TO SUBMERGENCE, SOIL WATERLOGGING AND OXYGEN SHORTAGE

Michael B. Jackson

INTRODUCTION

Ethylene and abscisic acid are two of five substances or groups of substances with established regulatory (hormonal) roles in plant development. The lack of detailed discussion here about the three remaining groups of hormones (gibberellins, cytokinins and auxins) does not imply that they are unimportant for the growth of inundated plants. Instead, it reflects a lack of experimental attention, despite some early and promising work with these compounds in waterlogged tomato and sunflower (Phillips, 1964; Burrows and Carr, 1969; Reid, Crozier and Harvey, 1969; Railton and Reid, 1973). Evidence that implicates ethylene in plant responses to over-wet conditions is particularly strong and comes from research from several laboratories working with different species and growth processes over a period of approximately 15 years. Studies with abscisic acid (ABA) are less extensive and have concentrated on stomatal closure. Only with the recent adoption of reliable physicochemical methods for ABA analysis, and the use of ABA-deficient mutants has the part played by this hormone in closing the stomata of waterlogged plants been demonstrated convincingly. Hormones such as ethylene and abscisic acid, possess several characteristics which make them likely mediators of developmental change initiated by aeration stress. First, they can be active in extremely small concentrations (e.g. ethylene is active in promoting leaf epinasty at 0.01 volumes per million, Leather, Forrence and Abeles, 1972). This suggests that quite small changes in hormone titre, induced quickly by environmental factors, can be physiologically significant. Secondly, only certain tissues or cells within a plant or organ are highly responsive to a particular hormone at a given time. Thus hormone effects are not located indiscriminately about the plant but instead are selective for particular tissues and locations. Such spatial precision is a prerequisite for any explanation of how excess water comes to modify specific morphogenetic processes. Hormones are also known to act very quickly. For example, applications of ABA to a leaf may close stomata within 5 min (Cummins, Kende and Raschke, 1971). This rapidity of action is necessary if hormones are to explain several effects of inundation which can be very fast (e.g. less than 10 min, Musgrave and Walters, 1974). At least one of the responses

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to inundation can also be reversed if water levels fall. It is therefore apposite that the effects of some hormones are reversible upon withdrawing treatment. The overriding characteristic of hormones that links them with aeration stress is the close visual similarity between several morphological consequences of flooding and those documented in the hormone literature as responses to application of these substances (see Jackson and Goss, 1978; Jackson and Drew, 1984; Reid and Bradford, 1984 for reviews). The extent to which hormone-mediated developmental phenomena aid survival by aeration-stressed plants is uncertain, although this seems likely on intuitive grounds. However, there is as yet little direct experimental evidence on this point.

ETHYLENE

Submerged or waterlogged plants have often been found to contain abnormally large amounts of ethylene (Kawase, 1971, 1972). There are four interrelated ways in which this enrichment may be brought about. (1) As a consequence of a water covering, the diffusive escape of ethylene from submerged plant tissues is reduced, which leads to accumulation of the gas (Burg and Burg, 1965; Musgrave, Jackson and Ling, 1972; Konings and Jackson, 1979). (2) Partial oxygen deficiency, caused by slow diffusion of atmospheric oxygen into submerged tissue, can stimulate ethylene synthesis in some species (Jackson, 1982; Metrau and Kende, 1983; Jackson, Fenning, Drew and Saker, 1985a). In deep-water rice, respiratory CO₂ entrapped within the submerged stem may further enhance the effect of hypoxia on ethylene synthesis (Raskin and Kende, 1984). (The possibility of ethylene-stimulated ethylene synthesis ('autocatalytic ethylene') in flooded plants does not seem to have been examined) (3) Total oxygen deficiency in roots can enrich the well-aerated aerial shoot (of tomato) with ethylene (Jackson and Campbell, 1976) by stimulating the rate of synthesis by the foliage (Jackson, Gales and Campbell, 1978), as a consequence of an increased flux of ethylene precursor (1-amino-cyclopropane 1-carboxylic acid-ACC) from anoxic roots to the aerated shoot (Bradford and Yang, 1980). (4) The ingress of ethylene produced in flooded soil (Jackson and Campbell, 1975). The likely significance of increased ethylene brought about in one or more of these ways is discussed below.

Fast underwater elongation

Aquatic and semi-aquatic plants of diverse taxa successfully colonize many areas subject to irregular fluctuations in the depth of water. A characteristic feature of these plants is an ability to elongate their coleoptile stems, or petioles more rapidly under water than above it (Arber, 1920; Funke and Bartels, 1937). This is thought to enhance survival by shortening the duration of total submergence, thereby minimizing physiological injury and interruptions to the life cycle. Faster extension in response to submergence has been measured within 10 minutes (Musgrave and Walters, 1974) and is reversible by re-floating. The plants, how-

ever, retain an ability to respond to submergence should the water rise again on one or more subsequent occasions (Musgrave et al., 1972; Jackson, 1982). A recent discovery that the stem of maize (*Zea mays*) elongates faster when plants are waterlogged (Jackson and Young, unpublished) raises the possibility that stems of some 'dry-land' monocots may also have evolved the ability to escape a modest depth of submergence by this means. Observations by Ku, Suge, Rappaport and Pratt (1970) and Jackson, Morrow and Osborne (1972), that ethylene treatment can promote extension growth, pointed the way to subsequent studies with *Callitricha platycarpa* (Musgrave, et al., 1972), *Ranunculus sceleratus*, *Hydrocharis morsus-ranae* and semi-aquatic fern *Regnellidium diphyllum* (Musgrave and Walters, 1974; Cookson and Osborne, 1978, 1979), *Nymphaoides peltata* (Malone and Ridge, 1983), rice coleoptiles (Atwell, Waters and Greenway, 1982; Raskin and Kende, 1983) and with the stems of deep-water rice (Metraux and Kende, 1983) that established unequivocally a submergence sensing and elongation-promoting role for ethylene. The evidence takes the form of (1) established similarities between ethylene and submergence effects (Ridge and Amarasinghe, 1984) report 20 angiosperm species that respond similarly to ethylene and submergence, (2) increased ethylene content of submerged plants that is demonstrably large enough to promote extension, (3) inhibition of the submergence response with chemicals that inhibit ethylene action (e.g. silver nitrate) or its synthesis (e.g. aminoethoxyvinylglycine). Interesting points include the necessity of other endogenous hormones, notably gibberellins (Musgrave, et al., 1972) or auxins (Cookson and Osborne, 1978; Ishizawa and Esashi, 1983) for ethylene action, and the enhancement of ethylene activity by carbon dioxide and hypoxia (Ku, et al., 1970). At the cellular level, ethylene-promoted extension is primarily the result of increased cell length and rate of elongation, but in *Nymphaoides peltata* (Ridge and Amarasinghe, 1984) and in stems of deep-water rice (Metraux and Kende, 1984) cell number is also increased. In rice coleoptiles, ethylene may promote cell extension by decreasing osmotic potentials to more negative values (Ishizawa and Esashi, 1984) whereas in *N. peltata* (Malone and Ridge, 1983) ethylene-increased cell extensibility via wall acidification seems to be involved. Ethylene also lessens cell wall rigidity in *R. diphyllum* but in this case without attendant proton extrusion (Osborne, 1984). In the last two species, longitudinal tension caused by buoyancy arising from the gas-filled aerenchymatous nature of the leaf or frond amplifies ethylene action (Musgrave and Walters, 1974; Ridge and Amarasinghe 1984), presumably by supplementing the influence of turgor pressure on cell wall expansion.

Aerenchyma formation in roots

Although an acceleration of extension offers a means of escape from submergence or soil waterlogging by upward-growing shoot tissues, such a strategy is clearly inappropriate to normally downward-growing organs such as roots. One means by which roots seem to avoid suffocation is by the possession of enlarged and interconnected internal gas-filled spaces (aerenchyma) formed

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by the lysigenous collapse of selected groups of cells. Rice roots begin to form aerenchyma in apical tissues with cells less than half-a-day old, even in well-aerated roots (Webb and Jackson, 1986). Consequently roots of this species seem 'pre-adapted' and there is little scope in these roots for an acceleration of aerenchyma development in response to impaired aeration (Jackson, Fenning and Jenkins, 1985b). In contrast, maize roots that have extended into water or poorly aerated media develop much more gas space than equivalent roots growing into well-aerated surroundings (Norris, 1913; McPherson, 1939; Sifton, 1945). Experiments reminiscent of the shoot-extension studies already described have implicated ethylene in this anatomical adaptation. Poorly aerated roots developing an extensive aerenchyma contain at least double the usual amount of ethylene (Drew, Jackson and Giffard, 1979), a result, in part, of increased rates of synthesis by roots exposed to partial oxygen shortage (Jackson, 1982; Jackson et al., 1985a). The promotion of aerenchyma by poor aeration can be simulated by applying small concentrations of ethylene (>0.1 vpm) to aerated roots (Drew et al., 1979; Konings, 1982) and inhibited by silver nitrate, an ethylene antagonist (Drew, Jackson, Giffard and Campbell, 1981; Konings, 1982) or by an inhibitor of ethylene biosynthesis (aminoethoxyvinylglycine) with activity that is reversible by applying the ethylene precursor ACC (Jackson et al., 1985a). Some other inhibitors of ethylene synthesis (cobalt chloride and amino-oxyacetic acid) also suppress aerenchyma formation, although the reversibility of their action, and thus specificity, is uncertain (Konings, 1982). The involvement of hormones other than ethylene in aerenchyma formation has yet to be firmly established. The report by Konings and de Wolf (1984) that the synthetic auxin naphthalacetic acid prevents aerenchyma formation suggests that endogenous auxin could oppose ethylene action, as it does in leaf abscission. There is also a possibility that deficiencies in nitrate (Konings and Verschuren, 1980) and phosphate (Drew and Saker 1983) brought about by a deprivation of oxygen may also encourage aerenchyma formation. Nothing seems to be known of any involvement of carbon dioxide, or of the enzymology of cell lysis that creates the gas-filled lacunae in the root cortex. A loss of tonoplast integrity is the earliest degenerative process reported in lysing cells of maize (Campbell and Drew, 1983). In rice, where ethylene does not promote aerenchyma, cell degeneration follows a different pattern with loss of cell wall structure preceding tonoplast rupture (Webb and Jackson, 1986).

Aerenchyma in organs other than roots

Roots are not the only plant parts to develop more extensive aerenchyma in wet conditions (Sifton, 1945); stem and leaf bases can also respond in this way. Limited evidence implicates ethylene in gas-space formation within the hypertrophic stem base of waterlogged sunflowers, an effect reproducible by applying ethephon (Kawase, 1974), a substance that forms ethylene gas when given to plants. The effect of ethylene on stem aerenchyma may be mediated by cell wall-degrading cellulase enzymes (Kawase, 1979, 1981). Any continuity of stem or leaf-base aerenchyma with root

aerenchyma would constitute an effective aeration pathway linking the root interior with the atmosphere.

Epinastic growth and leaf extension

Leaf epinasty results from faster growth on the adaxial side of the petiole than on the abaxial side, thus forcing younger leaves to roll up and the older leaves to adopt a more downward inclination. The resulting change in morphology superficially resembles wilting, although epinasty is actually brought about by turgor-requiring growth and wilting is not involved. Its acclimatic significance is uncertain but epinasty probably decreases evaporative demand by reducing the amount of radiant energy intercepted by the shoot. This probably helps to offset the tendency to wilt during early waterlogging when resistance to water uptake by roots is increased by oxygen shortage. Much experimental evidence implicates ethylene as a regulator of epinasty, at least in waterlogged tomatoes. This species is highly responsive and begins epinastic growth within 1-4 h of applying >0.01 vpm ethylene. Soil waterlogging can enrich the shoots with naturally produced ethylene within 24 h, when epinastic curvatures are developing fast (Kawase, 1972; Jackson and Campbell, 1975). This ethylene seems to be responsible for promoting epinasty since it can be slowed by application of inhibitors of ethylene action (carbon dioxide, benzothiadizole, silver nitrate) to the shoots (Jackson and Campbell, 1976; Bradford and Dilley, 1978). Faster synthesis in shoot tissue is the principal reason why more ethylene is present (Bradford and Dilley, 1978; Jackson *et al.*, 1978) and results from more ACC passing from anoxic roots to the shoots in the transpiration stream (Bradford and Yang, 1980). If the production of ACC in anoxic tomato roots is slowed by inhibitors such as amino-oxyacetic acid and aminoethoxyvinylglycine, root anaerobiosis no longer promotes leaf epinasty (Bradford, Hsiao and Yang, 1982), a result consistent with the need for faster ethylene synthesis in the shoot if epinasty is to develop in waterlogged tomato plants. Leaves of monocots such as maize do not become epinastic following waterlogging. However, elongation is inhibited, an effect easily reproduced by applying ethylene. In one recent study, endogenous ethylene has been implicated in the slowing of leaf extension by maize grown in non-aerated nutrient solution (Jackson, Drew and Giffard, 1981). The acclimatic value of this response may be to limit shoot size non-destructively to one more appropriate to a root system enfeebled by anaerobiosis.

ABSCISIC ACID

Despite an earlier view that waterlogging invariably causes wilting (Kramer, 1951; Kramer and Jackson, 1954,) it is becoming increasingly clear that in herbaceous (Sojka, Stolzy and Kaufmann, 1975; Jackson *et al.*, 1978; Bradford and Hsiao, 1982; Jackson and Kowalewska, 1983) and woody species (Pereira and Kozlowski, 1977; Kozlowski and Pallardy, 1984) foliar water deficiency is often avoided, at least during the first few days. Indeed leaf hydration

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can increase rather than decrease, in association with epinasty, stomatal closure, slower transpiration and less negative leaf water potentials (Jackson *et al.*, 1978). The case for involving ABA in stomatal closure (Jackson, 1985; Jackson and Hall, 1986) is based on the following evidence obtained using peas. During the first 24-30 h of flooding, foliar ABA concentrations increase before, or at the same time as, stomata begin to close. These increases are judged to be more than sufficient to close stomata since they exceed those required to decrease leaf conductance to water vapour when leaves are given exogenous ABA. Inhibitors of the synthesis or action of ABA are not available and thus verification experiments of the type described above for ethylene cannot be made. Instead, a mutant form of pea with impaired capacity for ABA synthesis has been utilized. This mutant plant and also its equivalent tomato mutant close their stomata only slightly when waterlogged, with little change in endogenous ABA (Jackson and Hall, 1986), adding credence to the view that increases in this hormone mediate stomatal closure during the early stages of waterlogging. The increase in ABA seen in waterlogged, non-mutant, plants probably comes about because leaves accumulate hormone that would normally have been exported with photosynthate to the roots. The adaptive significance of this ABA-mediated stomatal closure is readily gauged from the extremely severe and irreversible wilting that takes place within the first 24 h of waterlogging ABA-deficient mutants in atmospheres of less than 95 per cent relative humidity.

CONCLUSIONS

There can be little doubt that ethylene is inextricably involved in several responses to waterlogging or submergence. Each constitutes a stimulation of cell growth (even in aerenchyma formation, cells expand considerably prior to collapse). The number of species (mesophytic and hydrophytic) and tissues found to respond to ethylene entrapped by environmental water is increasing as research proceeds. The evidence thus far constitutes a most convincing case for implicating a hormone in plant response to environmental stress. The knowledge may help manage vegetation in wet places (Jackson, 1983).

A present role for ABA has been demonstrated in ensuring fast stomatal closure of plants subjected to sudden flooding of the soil. Even if this remains the only response to flooding that is regulated by ABA, its potential for drastically decreasing losses in shoot turgor during the first hours and days of soil waterlogging under conditions of high evaporative demand make it an important one in terms of survival value.

There is an obvious need to press ahead with studies of other hormones, taking advantage of recent improvements in hormone identification and quantification.

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Chapter Thirty-two

NUTRIENT UPTAKE AND ACCLIMATION TO SOIL WATERLOGGING AND OXYGEN SHORTAGE IN NON-WETLAND PLANTS

M.C. Drew

INTRODUCTION

Non-wetland crop species can experience temporary flooding or waterlogging in widely different climatic zones of the world. Such flooding may originate either from poor soil drainage following irrigation or heavy rain, or from a rising water-table because of net water movement into the soil profile from adjacent land (Van't Woudt and Hagan, 1957). When soil temperatures are high, which is often the case during irrigation in semi-arid climates, the concentration of dissolved oxygen in the soil water is exhausted, often within a few hours (Ioannou, Schneider and Grogan, 1977), with deleterious consequences for plant growth and yields. Even in more temperate climates in NW Europe, the concentration of oxygen in the soil water slowly declines and characteristic symptoms of waterlogging injury occur (Cannell and Jackson, 1981).

The decline in soil oxygen brings about a profound change in the physicochemical properties of the soil, including an accumulation of reduced inorganic compounds and organic metabolites (Gambrell and Patrick, 1978; Ponnampерuma, 1984), but for some years the view has been advanced that the primary and often principal cause of plant injury is the inadequate supply of molecular oxygen to the root system (Jackson and Campbell, 1976; Drew and Lynch, 1980). The essential role of oxygen in this context provides the rationale for the use of nutrient solution bubbled with sub-ambient oxygen concentrations or anaerobic (oxygen free) gases to simulate the shortage of oxygen known to occur in the soil. It is important to recognize however, that deoxygenated nutrient solution provides only a partial model of the oxygen-deficient soil: there are numerous, well-supported observations to show that plant injury or death is sometimes associated in the longer term with accumulation of reduced manganese or iron or even H_2S in the soil water, despite plant acclimation to the unfavorable environment (Drew and Lynch, 1980).

This chapter considers the interruption to the mineral nutrition of the plant that can occur under oxygen-deficient conditions, and its influence on the behavior of the shoot in cereal species. The changes in the plant that may improve the ability to obtain inorganic nutrients under oxygen deficient conditions, and therefore improve fitness under stress are also examined. The

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impairment in plant mineral nutrition is only one aspect of 'stress physiology' in plants with oxygen-starved roots - water stress, hormonal imbalance, inhibition of photosynthesis are others (Jackson and Drew, 1984). However, mineral nutrition clearly exerts a major role, especially for nitrogen.

NUTRIENT UPTAKE AND TRANSPORT TO THE SHOOTS IN 'UNADAPTED' ROOTS

Ion uptake into root cells and transport to the xylem, and hence the rest of the plant, depend directly or indirectly on energy derived from oxidative phosphorylation during aerobic respiration. Letey and Stolzy and their co-workers at Riverside, California (Letey, Stolzy, Blank and Lunt, 1961; Letey, Stolzy and Valoras, 1965) made it clear that in growing plants, flooding generally caused a decline in tissue concentrations of nitrogen, phosphorus and potassium. By contrast, the concentration of sodium frequently increased, suggesting a failure to exclude this non-essential ion. Although these aspects have been known for many years, the consequences for the physiology of the shoot, when supplies of inorganic nutrients (or their immediate organic derivatives) are inhibited, has received little attention.

When the roots of young barley or wheat plants are oxygen starved by soil flooding or by deoxygenation of the nutrient solution, the older leaves become prematurely senescent or chlorotic, resembling the typical symptoms of nitrogen deficiency (Drew and Sisworo, 1977, 1979; Trought and Drew, 1980a,b,c). At one time this chlorosis in flooded plants was put down to accumulation of (unspecified) toxins from the soil water, but the fact that it is induced in nutrient solution, and associated with a decline in nitrogen, phosphorus and potassium concentration in the senescing leaf, suggests that it is simply the consequence of an arrested energy-dependent ion transport. In wheat, there was little net transport of nutrients from the anaerobic roots, while nutrients were withdrawn from the older leaves and translocated to the younger ones apparently by way of compensation (Trought and Drew, 1980b,c): no such net redistribution was detected in the aerated controls in the same time span. It therefore appears that poor root aeration can induce early leaf senescence by failing to deliver to the leaves essential supplies of inorganic nutrients. This conclusion does not preclude the involvement of endogenous growth substances in regulating the redistribution pattern, but it suggests that mineral nutrition, at substrate levels, plays a primary role.

If mineral nutrition, or its interruption, is important as a determinant of flooding injury, it would be expected that the provision of an additional source of nutrient ions to the shoot would alleviate the injury. Two approaches to this were carried out: first, a divided root system was used, in which five or six seminal roots of wheat were in anaerobic nutrient solution, while a single root was maintained in either aerated distilled water or aerated nutrient solution (Trought and Drew, 1981). Plants in fully anaerobic solution or with the single root supplied with only

water, quickly developed symptoms of flooding injury: slow growth and leaf chlorosis. When the full complement of major nutrient ions was supplied to the single aerobic root, no symptoms of flooding damage appeared and growth was similar to that in fully aerobic controls. Comparable results were obtained in waterlogged soil with barley (Drew, Sisworo and Saker, 1979). Secondly, a variety of pretreatments designed to improve the nitrogen status of the plant, such as foliar feeding with urea, or 'preloading' the shoot by supplying roots with high concentrations of nitrate before the anaerobic treatment, helped retard leaf senescence during that treatment. Such results point to an important role for the supply of inorganic nutrients to the shoot during anoxia of the root, when its normal functions are inhibited.

Whether nitrate can exert a special role in plants during anoxia by acting as a terminal electron acceptor in place of molecular oxygen (Garcia-Novo and Crawford, 1973) remains unclear. No acceleration of nitrate reduction was found in anoxic barley roots; furthermore, little or no nitrate uptake occurred under these conditions, while the nitrate that was produced leaked from the cells into the medium and failed to become further reduced (Lee, 1978). On the other hand, ^{31}P -NMR of corn root tips showed that large additions of $\text{Ca}(\text{NO}_3)_2$ to the medium (25 mM) caused a slowing of the cytoplasmic acidosis (Roberts, Andrade and Anderson, 1985) associated with cell death in energy-starved cells (Roberts, Callis, Wemmer, Walbot and Jardetsky, 1984a; Roberts, Callis, Jardetsky, Walbot and Freeling, 1984b; see also Chapter 33). Whether this effect was specific to nitrate was not tested. Clearly, further work with a range of tissue, including those considered to be 'anoxia tolerant', is necessary.

FUNCTION OF ADVENTITIOUS, AERENCHYMATOUS ROOTS

Some days or weeks after the onset of flooding, depending on temperature and species, adventitious roots emerge from the base of the stem of many dry-land crops and grow into the oxygen-deficient medium (Jackson and Drew, 1984). The structure of these roots is frequently aerenchymatous, with prominent gas-filled cavities that run longitudinally in the cortex, and resembles that found in wetland species (Kawase, 1981). Whereas the wetland species often have a constitutive ability to form aerenchyma and, at least in rice, does not require oxygen shortage or enhanced ethylene concentrations to induce its formation (Jackson, Fenning and Jenkins, 1985) early emergence of adventitious roots in corn and the lysis necessary for aerenchyma formation are ethylene-promoted (see Chapter 31).

Because of the disruption to the root cortex in cell lysis amounting to 80 per cent of the cells in the mid-cortex in zones about 100 mm distal to the root tip (Drew, Chamel, Garrec and Fourcy, 1980), the ability of such roots to absorb and transport ions to the xylem was tested. The roots were induced to form aerenchyma and then compared with non-aerenchymatous ones, uptake taking place in the presence of air. Phosphate (at 10, 40 and 100 μM) and potassium (at 0.25 and 5.0 mM) were labelled

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with radioactive tracers and supplied together with other nutrient ions to a 4-12 mm segment located approximately 100 mm from the tip on intact roots (Drew and Saker, 1986). In no experiment was there any interference in ion transport (per unit root weight or volume) in aerenchymatous roots. Per unit length, aerenchymatous roots showed an enhanced uptake and transport, perhaps because of the smaller total size of the root system in plants previously exposed to sub-ambient oxygen concentrations.

The important feature is that such observations call in question the role of the root cortex in symplasmic ion transport to the xylem. The cortex has long been viewed as a collecting system, with ions moving from the free space of the cell walls across plasma membranes into the cytosol, prior to passage to the xylem via a continuous cytoplasm and plasmodesmata. Perhaps contrary to earlier views, the overall process is regulated more at the stage of unloading of ions from the symplast into the xylem than at the initial point of entry into the symplasm (Drew and Saker, 1986). Some intact cells remain to bridge the cortical lucunae, and it is possible that unusually rapid transport of ions takes place through these cells. Alternatively, electron probe X-ray microanalysis suggests that wall residues that persist after cortical cell lysis are still part of the free-space, so that radial diffusion can take place to the endodermis, followed by entry into the symplasm at that location (Drew and Fourcy, 1986). Whether aerenchymatous roots are adequate to maintain the mineral nutrition of the plant will depend on whether a sufficient number are induced to grow to replace fully the initial root system: additionally, it is implicit that sufficient oxygen is present, by internal gas movement, to sustain aerobic respiration. Roots of wetland species characteristically form tissues that retard the outward diffusion of oxygen in the older, distal zones of the root, while dry-land species, lacking this anatomy, tend to lose oxygen along the entire root by outward diffusion to the oxygen-deficient rhizosphere (Armstrong, 1979).

How effective is the formation of aerenchyma in improving the internal conduction of oxygen towards the root tip, where an adequate supply is essential for root growth and differentiation? One approach would be to quantify the longitudinal diffusion of oxygen using tracers with aerenchymatous and non-aerenchymatous roots (Barber, Ebert and Evans, 1962; Vartapetian, Andreeva and Nuritdinov, 1978). An alternative is to estimate longitudinal diffusion of oxygen from the shoot (in air) into the root by examining the extent of aerobic respiration in different zones along the root maintained in an anaerobic solution (Saglio, Raymond and Pradet, 1983), an inhibitor being included to suppress fermentation. In non-aerenchymatous, seminal roots of corn, the resistance to gaseous diffusion of the intercellular spaces, together with radial leakage of oxygen, resulted in appreciable diffusion over distances of only 80 mm. When adventitious roots were examined (Drew, Saglio and Pradet, 1985), aerenchyma was induced in some by bubbling the nutrient solution with 5 per cent (v/v) oxygen in nitrogen (air = 20.6 per cent oxygen), while others were bubbled with 40 per cent oxygen in nitrogen to insure that the tissue was fully aerobic. In these larger-diameter roots some longitudinal diffusion of oxygen must have taken place as far

as the meristem in roots of 210 mm in length since the ATP/ADP ratio of 0.8 was greater than in excised, anaerobically incubated apices (0.05). By contrast, apices of aerenchymatous roots showed an appreciably greater ATP/ADP ratio (1.8), equivalent to about 30 per cent of the respiration rate in fully aerobic apices (ATP/ADP between 3 and 5). Thus, aerenchyma assisted internal transport of oxygen in adventitious roots, but at distances of 210 mm there was clearly insufficient oxygen to maintain respiration fully. Obviously, estimates of energy metabolism obtained by extracting root segments are a mean value, perhaps disguising radial gradients in oxygen supply and aerobic respiration that may be occurring, especially within the stele, where the tightness of cell packing with few intercellular spaces would constitute a large resistance to gaseous diffusion. In root zones closer to the oxygen source (the shoot), ATP/ADP ratios were 3.2 in aerenchymatous roots, indicating that the entire segment was essentially aerobic. Such information strongly supports the view that sufficient oxygen would have moved longitudinally from the shoot to the root to have maintained respiration and thus energy-dependent radial ion transport in the roots of undisturbed plants in an oxygen-deficient medium.

METABOLIC ADAPTATION TO OXYGEN DEFICIENCY

An intriguing question concerning the success of wetland species is the apparently specialized metabolism that allows truly anoxia-tolerant tissues (Barclay and Crawford, 1982) to maintain viability, or even show limited growth under conditions that are lethal to intolerant cells. A large body of information points to glycolysis and ethanolic fermentation as the principal pathway for synthesis of ATP under anoxia, with leakage of ethanol to the aqueous medium, or its transpiration, as the means for ridding cells of the end product (Davies, Grego and Kenworthy, 1974; Smith and apRees, 1979; Bertani, Brambilla and Menegas, 1980; Saglio, Raymond and Pradet, 1980; Bertani and Brambilla, 1982; Rumpho and Kennedy, 1983; Roberts *et al.*, 1984a). Adequate supplies of carbohydrate would be necessary to sustain anaerobic metabolism over weeks or months, and it is noteworthy that the submerged, anoxia-tolerant rhizomes of Schoenoplectus lacustris are storage organs packed with starch (Monk and Brändle, 1982). The provision of substrates for glycolysis is unlikely to be the only explanation of anoxia tolerance (Barclay and Crawford, 1983): one contributory factor could possibly be in terms of the phospholipid composition of the cell membranes (Hetherington, Hunter and Crawford, 1982). In coleoptile and mesocotyl of Echinochloa crus-galli var. oryzicola, anoxia tolerance seems to be associated with the maintenance of a higher energy metabolism, mitochondrial structure, and Krebs cycle enzymes, and an intense lipid metabolism (see Chapter 30).

In anoxia-intolerant roots of corn or rice suddenly exposed to anaerobic conditions, the maintenance of energy metabolism is closely associated with glycolysis and fermentation (Bertani, *et al.*, 1980; Saglio *et al.*, 1980). In excised root tips, these become

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limited by a supply of easily resired substrate. Addition of glucose can sustain energy metabolism for many hours (Saglio et al., 1980) and maintain mitochondria in an apparently normal structure in roots of rice and pumpkin (Vartapetian et al., 1978).

In nature, cells are rarely suddenly exposed to anaerobic conditions, but rather the equilibrium oxygen partial pressure gradually declines in hours or days. The possibility remains that a gradual exposure to oxygen deficiency induces a metabolism that is better adapted to anoxia. In recent experiments (Saglio, Drew and Pradet, unpublished) we found that exposure of intact plants of Zea mays to a low oxygen partial pressure (5 per cent oxygen in nitrogen) raised the subsequent tolerance to anoxia of the excised root tips. Under anaerobic conditions, energy metabolism was maintained at a level intermediate between fully aerobic cells and those suddenly made anoxic. Comparison of the metabolism of these 'induced' roots with that of anoxia-tolerant tissues in other species will be valuable in identifying pathways conductive to increased cell survival.

Although many dry-land crop plants show poor tolerance to flooding and oxygen stress compared to wetland species, physiological and biochemical changes take place in dry-land species that confer a degree of tolerance. Close comparison between the biochemistry of wetland and dry-land species will improve understanding of strategies for the improvement of flood-sensitive crops by genetic means.

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Chapter Thirty-three

CYTOPLASMIC ACIDOSIS AND FLOODING TOLERANCE IN CROP PLANTS

Justin K.M. Roberts

INTRODUCTION

The metabolically active tissues and organs of most crop species can survive only short periods of extreme hypoxia (Jackson and Drew, 1984). We have been interested in the factors, both internal and external, that may influence how long such tissues can withstand extreme hypoxia before irreversible tissue damage occurs (Roberts, Callis, Jardetsky, Walbot and Freeling, 1984a; Roberts, Callis, Weimner, Walbot and Jardetsky, 1984b). Because these plant tissues at some point in time inevitably succumb to extreme hypoxia, internal and external factors only affect the rate at which tissue damage accumulates following the onset of hypoxia. The factors cannot cause death, they can only influence or determine the time of death.

The role of cytoplasmic pH in determining the tolerance of tissues of crop plants to hypoxia is considered here from three points of view. First, can cytoplasmic acidity result in earlier death of hypoxic roots? Second, when is the degree of cytoplasmic acidosis during hypoxia altered, and when does increased acidosis correlate with earlier death? Third, how and when can cytoplasmic pH of flooded crop plants be manipulated to influence their tolerance of flooding under field conditions?

QUANTIFYING TOLERANCE OF HYPOXIA IN ROOT TIPS

The viability of excised root tips has been assessed by measuring their ability to grow (increase in fresh weight) (Roberts et al., 1984a). When samples of root tips are made hypoxic for increasing periods of time, the capacity to grow decreases, eventually to zero. Such measurements permit us to determine when root tips die under hypoxia. This determination permits us to see if various metabolic phenomena might be determinants or consequences of, or are unrelated to, the time of death.

**EXPERIMENTALLY INDUCED CYTOPLASMIC ACIDOSIS RESULTS
IN PREMATURE DEATH OF HYPOXIC MAIZE ROOT TIPS**

The degree of cytoplasmic acidosis in hypoxic maize root tips can be manipulated experimentally using carbon dioxide, provided externally or generated internally during ethanolic fermentation (Roberts, Wemmer, Ray and Jardetzky, 1982; Roberts *et al.*, 1984). When the severity of cytoplasmic acidosis was increased, death occurred earlier (Roberts *et al.*, 1984a). Hence, a causal link between cytoplasmic acidosis and the time of death was established in hypoxic maize root tips: if severe acidosis occurs, earlier death will occur. The principal ambiguity remaining after this result is that it tells us nothing about the relative importance of cytoplasmic pH in determining the time of death in hypoxic root tips not exposed to carbon dioxide. Other conditions that affect both viability and cytoplasmic pH are described below.

CYTOPLASMIC ACIDOSIS DUE TO LEAKAGE OF VACUOLAR H⁺

Severe cytoplasmic acidosis, and death, eventually occur in maize root tips that are not exposed to excess carbon dioxide (Roberts *et al.*, 1984a). In the first few minutes of hypoxia, cytoplasmic acidosis is due largely to fermentation to lactic acid (Roberts *et al.*, 1984b). Over longer periods of hypoxia, significant leakage of protons from vacuole to cytoplasm is apparent, for a rise in vacuolar pH occurs as cytoplasmic pH falls (Roberts *et al.*, 1984a). The collapse in the cytoplasmic-vacuolar pH gradient may be due to both an inhibition of the tonoplast H⁺-ATPase, and an increase in the H⁺-permeability of the tonoplast (Roberts, 1985). The leakage of acid from vacuole to cytoplasm does not result from a general loss of cell integrity for, in maize root tips, leakage of vacuolar H⁺ occurs before leakage of vacuolar inorganic phosphate is observed (Roberts *et al.*, 1984a).

Leakage of acid from vacuole to cytoplasm occurs earlier in hypoxic pea roots, compared to maize, and may explain the lower tolerance that peas have of hypoxia (Roberts *et al.*, 1984a). Of course, this species comparison, and others (Roberts, Andrade and Anderson, 1985), speak largely to the generality of the role of cytoplasmic pH in determining tolerance of hypoxia among crop species. In no way do these comparisons address the importance of cytoplasmic pH, relative to other factors, in determining survival of hypoxic roots of a particular crop species. For example, the tonoplast of hypoxic peas appears to be leakier to substances other than protons (e.g. P_i), compared to maize (Roberts *et al.*, 1984a). Clearly, individual species and tissues exhibit unique features that may obstruct the path to a general theory of flooding tolerance.

**CYTOPLASMIC ACIDOSIS IS RETARDED, AND VIABILITY IS
PROLONGED, IN MAIZE ROOT TIPS EXPOSED TO NITRATE**

Cytoplasmic acidosis determines, at least in part, how long root tips (not exposed to carbon dioxide) survive under hypoxia. For if

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cytoplasmic acidosis is reduced by treatment of roots with nitrate, viability under hypoxia is prolonged (Roberts et al., 1985). While cytoplasmic pH fell less in nitrate-treated root tips, vacuolar pH actually increased more than in controls (Roberts, 1985), indicating that leakage of acid from vacuole to cytoplasm per se does not lead to earlier death - only when cytoplasmic acidosis is increased.

ALCOHOL DEHYDROGENASE (ADH), CYTOPLASMIC ACIDOSIS, AND VIABILITY IN HYPOXIC MAIZE ROOT TIPS

Mutant maize root tips, with greatly reduced levels of ADH, exhibit extreme cytoplasmic lactic acidosis early in hypoxia (Roberts et al., 1984a,b), and die much more quickly than wild-type tissue (Roberts et al., 1984a). This result supports the notion that cytoplasmic pH can determine tolerance of hypoxia in maize roots. Although the concentration of ADH appears to limit production of ethanol, and so cytoplasmic pH regulation, in the mutant, there is no evidence that this is the case in wild-type maize roots (cf. Alpi and Beevers, 1983).

RELEVANCE OF THE ABOVE STUDIES TO FLOODING TOLERANCE OF MAIZE IN THE FIELD

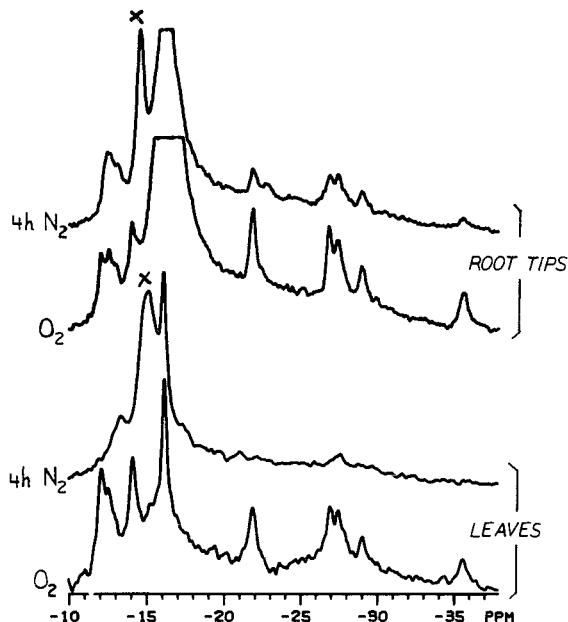
Maize roots are tolerant of root flooding (Yu, Stolzy and Letey, 1969; Purvis and Williamson, 1972). This tolerance is attributable partly to the higher oxygen tensions usually encountered in flooded corn fields, compared to laboratory experiments employing oxygen-free gas cylinders. The development of aerenchyma in hypoxia roots (Drew, 1979) also diminishes the severity of hypoxia in submerged roots. Hence, root death is not inevitable in the field, as it is in our hands.

However, we are currently exploring the possibility that cytoplasmic pH may determine in part how low maize leaves survive when submerged. This avenue of research is based on two observations. First, wild-type maize leaves show some similarities to mutant maize root tips that lack ADH. Thus, leaves have low levels of ADH (Scandalios and Felder, 1971), and undergo more severe cytoplasmic acidosis during hypoxia, compared to wild-type roots (Figure 33.1), and die more rapidly under anoxia (Okimoto, Sachs, Porter and Freeling, 1980). In fact, maize leaves can survive only a few tens of hours of submergence in water that is exposed to air. Second, tolerance of submergence is increased in leaves from plants that are fed nitrate, while it is decreased in leaves from plants that are provided with ammonium prior to flooding. We are examining now whether the effects of these fertilizers on flooding tolerance can be attributed to differences in cytoplasmic pH.

LINKS BETWEEN CYTOPLASMIC ACIDOSIS AND VIABILITY

Figure 33.2 presents some of the phenomena that occur when tissues such as maize root tips experience hypoxia. The arrows

Figure 33.1: ^{31}P -NMR spectra of 5-day-old leaves, and 2-day-old root tips of maize, perfused under oxygenated or hypoxic conditions. The greater shift of the peak x to the right in the spectrum of the leaf under nitrogen indicates greater acidification of the cytoplasm in this tissue, compared to root tips



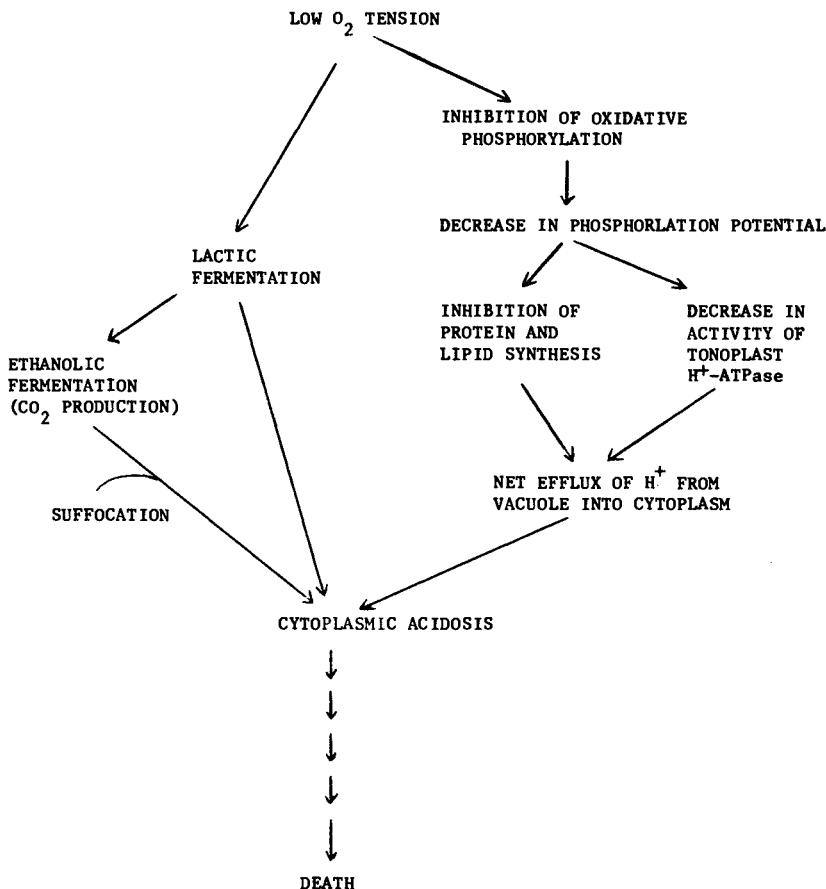
indicate sequences of phenomena, in which particular events are seen as leading to later phenomena. Certain factors, such as cytoplasmic pH, appear to be linked to the time of death, whereas other processes, such as glycolytic rate, affect viability in no obvious way (Roberts et al., 1984a, 1985). Still, descriptions of the mechanisms by which cytoplasmic pH might determine viability in hypoxic plant cells are speculative. Our attention is drawn to the fact that biosynthesis is drastically reduced in hypoxic tissues, while degradative processes continue. This imbalance would explain why death is inevitable in such hypoxic tissues. It is possible that low cytoplasmic pH accelerates degradative processes; this would decrease the length of time a cell could experience extreme hypoxia before irreversible loss of cell integrity.

ACKNOWLEDGEMENTS

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Figure 33.2: Interactions between metabolic phenomena following the onset of hypoxia in plant tissues



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Chapter Thirty-four

THE RELATIONSHIP OF SOIL PARAMETERS AND ROOT METABOLISM TO PRIMARY PRODUCTION IN PERIODICALLY INUNDATED SOILS

Irving A. Mendelsohn and David M. Burdick

INTRODUCTION

Hydrology is the dominant forcing function in wetland ecosystems (Gosselink and Turner 1978). Through its direct effect on soil waterlogging, the dynamic hydrologic environment controls soil physicochemical status, sedimentation rates, salinity, nutrient cycling, decomposition, and faunal and microfloral activities. Thus soil waterlogging controls the interaction of soil and root processes which, in turn, influence growth (Figure 34.1). Although wetland vegetation is highly productive, the roots of these plants often experience severely reduced soil conditions, lack of oxygen, and toxic compounds as a result of soil waterlogging. This chapter emphasizes the linkage between growth responses and waterlogging-induced changes in root processes of wetland vegetation. While not exhaustive, the examples in Tables 34.1-34.5 illustrate the major soil-root interactions which influence growth. In addition, we present a case study describing how hydrologically induced changes in soil parameters affect root processes and ultimately growth and productivity of *Spartina alterniflora*, the dominant intertidal salt marsh angiosperm of the Atlantic and Gulf Coasts of the United States.

ROOT PROCESSES AFFECTED BY SOIL WATERLOGGING

Energy Metabolism

Although this topic has received attention in several reviews (Pradet and Bomsel, 1978; Davies, 1980; Pradet and Raymond, 1983; Hook, 1984; Jackson and Drew, 1984), much of the research concerned with the impacts of waterlogging on root energy metabolism has focused on a few agricultural species. In experiments with maize and rice, decreasing supplies of oxygen below the critical oxygen pressure (COP: the oxygen concentration below which aerobic respiration is reduced) result in a depression of the root energy status (Saglio, Raymond and Pradet, 1983) as indicated by the adenylylate energy charge ratio (AEC: the ratio of phosphorylated adenine nucleotides to the total adenine nucleotide pool). However, the AEC of seeds, roots, and rhizomes of more waterlogging-tolerant species placed in anoxia partially rebounds

Figure 34.1: Changes in the soil environment due to soil waterlogging affect specific root processes which in turn affect plant growth

SOIL WATERLOGGING

CAUSES CHANGES IN
SOIL



PHYSICAL PROPERTIES
GASSES
AVAILABLE ELEMENTS AND REDOX STATE
ORGANIC COMPOUNDS
MICROBIAL COMMUNITY AND FUNCTION
FAUNAL COMMUNITY

AND THUS AFFECTS SPECIFIC
ROOT PROCESSES



ENERGY METABOLISM
CARBOHYDRATE METABOLISM
WATER UPTAKE
NUTRIENT UPTAKE
HORMONAL PROCESSES
RHIZOSPHERE DEVELOPMENT

WHICH IN TURN AFFECT
PLANT GROWTH
AND PRODUCTIVITY

Table 34.1: Growth responses to changes in energy and carbohydrate metabolism due to soil waterlogging of selected wetland plants

Species	Treatment	Change in metabolism ^a	Change in growth	Reference
Rice	N ₂ /sand culture	PDC and ADH increase at 0% [O ₂]	No change in root or shoot	Wignarajah et al. (1976)
Rice	N ₂ /added glucose	Anaerobic resp. w/added glucose	Increased survival time	Vartapetian et al. (1977)
Rice	4 cm H ₂ O over seeds	EtOH increases in solution	No root growth	Avadhani et al. (1978)
Rice	N ₂ for 48 h	Pasteur effect w/EtOH ferm.	No growth but tips viable	Bertani et al. (1980)
Rice	Several [O ₂]	ADH increases <10% [O ₂]	Shoot decrease <10% [O ₂]	Bertani & Brambilla (1982)
Rice and <i>Echinochloa</i> complex	Seeds or whole seedlings in several paths important; CO ₂ + EtOH [O ₂] up to 7 days	Glycolysis, pentose-phosphate but no Pasteur effect; delay and depression in respiration	No root growth but survival	Rumpho & Kennedy (1981)
3 Wetland spp.	Rhizomes in 0% O ₂ and several [CO ₂] ^b	Respiration reduced	Retained viability	Rumpho & Kennedy (1983)
13 Wetland species	Flooding in sand for 1 month	Control of metabolic rate	Growth + survival	Crawford (1966) (1967)
<i>Glyceria maxima</i>	Several [O ₂]	Carbon metabolism changes	Biosynthesis for growth stops at 2% [O ₂]	ApRees and Wilson (1984)
<i>Spartina alterniflora</i>	Et controlled 20 days	ADH rises with falling Eh	No change in root or shoot	DeLaune et al. (1984)

Table 34.1 (continued)

5 salt marsh spp.	100 micro M sulfide spp.	$\frac{0}{2/4}$ uptake reduced in all spp. w/low metallo-enz. act.	1: no effects; 1: root growth fell; 3 had lower growth + chlorosis	Havill et al. (1985)
<u>Pinus contorta</u>	Anoxic hydroponics	Glycolytic control of EtOH prod.	Growth cont. in leading shoots	Crawford & Baines (1977)
<u>Pinus contorta</u>	Flooding	Changes in root [sugar]	Shoot growth sustained	Vester & Crawford (1978)
<u>Nyssa sylvatica</u>	Flooding 3 populations	ADH activity + malate levels rise in tolerant population	Roots replaced but equal production	Keeley (1977)(1979)
5 tropical trees	Flooding 1 month	5 had Pasteur effect; but carbohydrate metabolisms differ	3/5 spp. continued shoot growth	Joly & Crawford (1982)
<u>Betula nigra</u>	N_2 gas 18 days	AEC falls after 6 days; ADH increases	Survival w/leaf chlorosis cytochrome oxid. falls	Tripepi & Mitchell (1984a)
<u>Acer rubrum</u> and <u>Betula nigra</u>	Flooding 1 month	Capacity for aerobic respiration falls	No change in <u>A.rubrum</u> ; decreased <u>B.nigra</u> survives but growth falls	Tripepi & Mitchell (1984b)

Note: a, PDC = pyruvate decarboxylase; ADH = alcohol dehydrogenase; AEC = adenylylate energy charge ratio

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after initially declining, apparently due to an increase in alcoholic fermentation (Pradet and Bomsel, 1978; Monk and Braendle, 1982; Rumpho, Pradet, Khalik and Kennedy, 1984). Furthermore, often drastic reductions in root AEC occur when the capacity to accelerate ethanol fermentation does not exist (Roberts, Callis, Wemmer, Walbot and Jardetsky, 1984a) or is eliminated by inhibitors or a lack of substrate (Saglio et al., 1980, 1983).

Declines in root and rhizome energy charge ratios in wetland species have been associated with root hypoxia in laboratory experiments (bulrush: Monk and Braendle, 1982; rice: Saglio, Rancillac, Bruzan and Pradet, 1984; river birch: Tripepi and Mitchell, 1984a) and under natural field conditions (*Spartina*: Mendelsohn, McKee and Patrick, 1981). As was found for agricultural species in the laboratory, decreases in root AEC associated with decreases in oxygen availability to the root (measured as decreases in soil redox potential) were partially reversed with increases in alcoholic fermentation (measured as ADH activity) for *Spartina alterniflora* (Mendelsohn et al., 1981; Mendelsohn and McKee, 1986). No research was found that showed a direct or a strong correlative link between root hypoxia and growth in wetland species via energy metabolism (Table 34.1), but Monk and Braendle (1982) do suggest that the upwardly stabilized AEC observed after two days in bulrush rhizomes under anaerobic treatment (supported by accelerated anaerobic metabolism) can sustain slow shoot growth as observed by Crawford (1982b). Other research linking energy metabolism with anoxia include reversible and irreversible damage of the mitochondrial membranes involved in aerobic respiration (Vartapetian, Andreeva, Kozlova and Agapova, 1977; Vartapetian, Zakhmylova and Generozova, 1985), the coupling of carbon and nitrogen paths to glycolysis by means of NAD cycling (Kennedy, Rumpho and VanderZee, 1983; Garcia-Novo and Crawford, 1973), and the decrease in energy from ATP hydrolysis available to drive cellular processes (Roberts, Callis, Jardetsky, Walbot and Freeling, 1984b) under anaerobiosis.

Carbohydrate Metabolism

Changes in root carbohydrate metabolism due to waterlogging or anoxia are mainly caused by oxygen deprivation (reviewed in Davies, 1980; Crawford, 1982a,b; Hook, 1984; Jackson and Drew, 1984), but can also be affected by increased CO₂ concentration in the root as well (Zemlianukhin and Ivanov, 1978; Crawford, 1982b; Chang, Hammett and Pharr, 1983). A decline in root oxygen availability disrupts the flow of photosynthate from shoot to root (Schumacher and Smucker, 1985) which is necessary to support root respiration (Vartapetian et al., 1978). The loss of solute translocation may result from the effect of low oxygen concentrations in the root on energy metabolism since this is an energy-dependent process, but evidence to the contrary is reviewed by Kozlowski and Pallardy (1984). During root anoxia, decreases in substrate availability for carbohydrate metabolism have been implicated in: changes in mitochondrial ultrastructure (Vartapetian et al., 1985); decreases in anaerobic metabolism and failure to maintain ATP levels (Saglio et al., 1980); and decreased growth

and viability following the anaerobic episode (Webb and Armstrong, 1983). More fundamentally, lack of oxygen results in cessation or severe restriction of the tricarboxylic acid (TCA) cycle (Jackson and Drew, 1984; Kennedy *et al.*, 1983) since NAD, which is required for reduction by the TCA cycle, is not recycled through NADH oxidation once the cytochrome system has ceased to operate.

All wetland species examined to date possess the ability to ferment ethanol, and some species accelerate glycolysis under hypoxia (Pasteur effect) to maintain ATP levels (rice: Bertani, Brambilla and Menegus, 1980; river birch: Triepi and Mitchell, 1984a). The accumulation of ethanol may be toxic (Crawford and Zochowski, 1984; but see Jackson, Hermand and Goodenough, 1982), and wetland species that cannot easily dispose of this metabolite (in thickened roots, tubers, rhizomes, and germinating seeds) seem to have developed the ability to control glycolysis (Crawford, 1982a,b). This ability has been observed in waterlogging-tolerant trees of temperate climates (Crawford, 1976), and may be thought of as a dormancy period lasting until the hypoxic stress has passed (Raymond and Pradet, 1980).

Mineral deficiencies caused by soil flooding may reduce activities of enzymes involved in carbohydrate metabolism that require specific metal cofactors for activation. Zinc is a cofactor for alcohol dehydrogenase (ADH), which converts acetaldehyde into ethanol. ADH activity in flooded rice roots, believed to support increased fermentation during root hypoxia, was depressed if Zn availability was decreased (Moore and Patrick, *in press*).

Water Uptake

The maintenance of photosynthetic rates, crucial to continued growth and productivity, depends upon high stomatal conductance which provides the necessary CO₂ for fixation. Paradoxically, waterlogging often produces plant symptoms similar to those seen under drought conditions: closing of the stomates resulting in decreased CO₂ uptake and transpiration, declining plant water potential, and even wilting (for recent reviews, see Jackson, 1983; Kramer, 1983; Jackson and Drew, 1984). These symptoms occur once waterlogging reduces water uptake at the root-soil interface; a manifestation of increased root resistance (*i.e.* decreased root permeability; Kramer, 1983).

Waterlogging-tolerant species often show little or no symptoms of drought stress upon waterlogging or anaerobiosis (rice: Tomar and Ghildyal, 1975; *Quercus palustris*: Black, 1984). Root permeability seems to be maintained either through internal oxygen supplies (Tomar and Ghildyal, 1975) or a favorable energy balance due to metabolic adaptation. No work has been performed on the water relations of wetland herbs or grasses that shows if root permeability to water uptake decreases with the cessation of aerobic metabolism of waterlogged plants, or if it can be maintained with the energy derived from an accelerated glycolysis. In plants lacking roots adapted to waterlogging (aerenchymatous and/or adventitious roots), either depressed or elevated plant water potential is usually noted in waterlogged treatments, accompanied

Table 34.2: Effects of flooding on water uptake and associated growth responses of selected wetland plants

Species	Treatment	Change in water relations	Change in growth	Reference
<u><i>Populus deltoides</i></u>	Seedlings flooded 4 then drained 1 week	Decrease in transpiration w/o decrease in turgor pressure	Photosynthesis falls 50% but shoot growth continued	Regehr <u>et al.</u> (1975)
5 tree species	Seedlings flooded 5 weeks	Stomatal closure in 3 days w/o leaf water stress; 2 spp. affected less	Root growth inhibited; leaf senescence in 3 less tol. spp.	Pereira and Kozlowski (1977)
<u><i>Fraxinus pennsylvanica</i></u>	Seedlings flooded 5 weeks	Stomatal closure, plants making adventitious roots opened stomates in 15 days	Reduced growth in roots, stem and leaves; leaf death	Sena-Gomes and Kozlowski (1980b)
<u><i>Platanus occidentalis</i></u>	Seedlings flooded 5 weeks	Stomatal closure with stem C ₄ leading to adventitious root production	Reduced growth in roots stem and leaves; root death; fall in root/shoot ratio	Tang and Kozlowski (1982)
3 conifer species	Seedlings flooded 4 days	None in flood tolerant sp. transpiration 50% in other 2	None in flood tolerant sp. Photosynthesis drops 50% shoot growth falls w/in 5 hours	Zaerr (1983)
3 <u><i>Pyrus</i></u> species	Seedlings in N - gassed liquid media for about 5 weeks	- Stomatal closure in 1 week, root conductivity falls at 3 weeks in all spp.; leaf water stress in least tolerant species	Slight chlorosis in 2 tolerant species wilting, defoliation, root death in least-tolerant species	Andersen <u>et al.</u> (1984)

Table 34.2 (continued)

<u>Acer saccharinum</u>	3- and 12-month-old seedlings flooded 4-8 weeks	Transpiration falls w/stomatal closure. Increased water use efficiency in year old seedlings when flooded	Reduced root, stem and leaf biomass and height; Photosynthesis falls in 3 month old seedlings	Petersen and Bazzaz (1984)
<u>Quercus palustris</u>	Flooded dormant season	None	None	Black (1984)
	Flooded near end of growing season	Stomatal closure: day 5+6, recovery: day 10, soil plant water resistance normal when measured on day 14	Leaf senescence 14 days early	
<u>Salix nigra</u> and <u>S. exigua</u>	2 years continuous flooding	None in leaf conductance or xylem water potential	In 2nd year: less flowers, acorns abort, leaf senescence 14d early	
	Flooded 36 h with lights on	Leaf conductance and water potential fell w/in 36 h	Wilting	Dionigi et al. (1985)
<u>Liquidambar styraciflua</u>	3-year-old seedlings flooded 9 days	Decrease in transpiration w/o decrease in xylem pressure potential	Photosynthesis reduced 77%	Pezeshki and Chambers (1985)

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by stomatal closure and increased root resistance to water uptake (Kozlowski and Pallardy, 1984).

Water relations research on wetland species has been performed primarily on woody angiosperms and gymnosperms. Significant declines in several aspects of root and shoot growth and changes in development due to waterlogging have been found by some workers, while others have found no or minor differences in plants tolerant of waterlogging (Table 34.2). Ultimately, long-term survival is dependent upon continued aeration of the root system, either through anatomical modification or adventitious roots growing in the inundated soil or water, so that root resistance to water uptake is reduced and hormonal communication between root and shoot is restored (Holder and Brown, 1980; Jackson and Drew, 1984; Reid and Bradford, 1984; Tsukahara and Kozlowski, 1985). In his review of waterlogging tolerance in trees, Gill (1970) stressed the importance of flooding length, intensity and seasonality and tree age and conditioning with regard to which species were most tolerant to waterlogging. Coutts (1981) extended these concepts to hypothesize different mechanisms inducing stomatal closure depending upon length and seasonality of waterlogging using Sitka spruce seedlings.

Nutrient Availability

Nitrogen. Waterlogging often increases nitrogen uptake in wetland species (bottomland hardwood trees: Hosner and Leaf, 1962; rice: Islam and Islam, 1973; general: Kozlowski and Pallardy, 1984), but sometimes soil waterlogging is associated with no change (rice: Jugsujinda and Patrick, 1977), or an inhibition of nitrogen uptake (bottomland hardwood trees: Dickson, Broyer and Johnson, 1972; *Spartina*: Morris, 1984). In a comparison of four species that form a natural topographic zonation pattern in periodically waterlogged dune slacks, nitrogen uptake and translocation was inhibited by soil waterlogging in all but the species normally occupying the lowest sites; and the inhibition was in order of increasing elevation (Schat, 1984; Table 34.3). Nitrogen uptake and assimilation is believed to be an energy-requiring process (Luttge and Higinbotham, 1979). In both wetland and agricultural species, the effect of low oxygen availability on ATP production was believed to be the key factor in reducing nitrogen uptake (Drew and Sisworo, 1979; Morris and Dacey, 1984; Schat, 1984). Besides a lack of oxygen, increased salinity or sulfide levels in waterlogged soils may interfere in nitrogen uptake (Garcia-Novo, 1976; Morris, 1984) or allocation (Cavalieri and Huang, 1981).

Phosphorus. Phosphorus availability usually increases with waterlogging of the soil (Gambrell and Patrick, 1978; Ponnampерuma, 1984). A large-scale flooding event in a Florida freshwater marsh mimicked the effect of phosphorus fertilizer application on shoot biomass and concentration of P in the tissues (Table 34.3), 'presumably due to the release of P from' the waterlogged soil (Bayley, Zoltak, Hermann, Dolan and Tortora, 1985). Phosphorus from floodwaters was associated with increased photosynthesis and

Table 34.3: Flooding effects on nutrient, salinity and mineral toxin uptake in selected wetland plants and their associated growth response

Material	Treatment	Change in uptake due to flooding	Growth response due to change in root uptake	Reference
Rice	Flooding vs. alternate flooding and draining	N uptake falls, especially if >1 alternation	Growth and grain yield fall with number of alternations	Patrick <u>et al.</u> (1967)
Rice	Hydroponics w/aerobic + anaerobic, pH=5,6,7,8	Aerobic: fall in Zn, rise in Fe at pH ₅ equal for P, NH ₄ ⁺	Root and shoot growth fall at pH 5	Jugsujinda and Patrick (1977)
8 salt marsh species	Flooding and salinity factorial	None	No synergistic effects	Cooper (1982)
4 dune slack species	Flooding and submerging	N,P,K and uptake reduced in 3 spp.	Size of decreases in growth in order of natural zonation	Schat (1984)
4 salt marsh species	Species and S ⁻² distribution in marsh 1mM S ⁻² hydroponics	Unknown Unknown	Only <u>Salicornia</u> colonizes and grows in high S areas Growth falls in all but <u>Salicornia</u>	Ingold and Havill (1984)
5 salt marsh species	Flooding - salinity factorial in silt and peat	No change in Na metabolism	Growth increased due to flooding	Snow and Vince (1984)
15 salt marsh species	Flooding-salinity factorial	None	Growth increased in 2 low marsh spp.; equal for 13 spp.	Rozema <u>et al.</u> (1985a)
Fresh marsh species	P addition in wet in plot and dry years	P uptake increases in plot w/o P in wet year	Production increased in plots w/o P in wet year	Bayley <u>et al.</u> (1985)

Table 34.3: (continued)

Material	Treatment	Change in uptake due to flooding	Growth response due to change in root uptake	Reference
<u>Erica tetralix</u> and <u>E.cinernea</u>	Flooding 8 weeks	Greater Fe and Mn increases in <u>E.cinernea</u>	No growth, root and plant death greater in <u>E.cinernea</u>	Jones and Etherington (1970)
<u>Empetrum</u> <u>nigrum</u>	Observations in wet and dry years	Aluminium availability and uptake higher in wet year	Increased abundance in dry year: toxic [Al] lower	Bell and Tallis (1974)
<u>Pinus taeda</u>	Seedlings flooded media pH 4-5	Fe, Mn, Zn, Na uptake in shoot increased	Reduced growth	Hook <u>et al.</u> (1981)
<u>Pinus taeda</u>	Flooding-phosphorus factorial	Flooding: P uptake decreased P addition: P uptake increased	Reduced growth Increased growth	McKee <u>et al.</u> (1984)

aboveground biomass in Taxodium distichum (Brown, 1981). On the other hand, waterlogging has led to decreases in P uptake in species that are relatively intolerant to waterlogging (Drew and Sisworo, 1979; Schat, 1984), perhaps due to root deterioration or an energy requirement of this process. In addition, the precipitation of P by Fe (made more available under waterlogged conditions) has been suggested to reduce P uptake and biomass accumulation of Pinus taeda (McKee, Hook, De Bell and Askew, 1984; McKevelin et al., unpublished). Among relatively waterlogging-tolerant species, no differences in phosphorus uptake were shown between aerobic and anaerobic treatments in rice (Jugsujinda and Patrick, 1977) or drained and waterlogged treatments in Samolus valerandi (Schat, 1984; Table 34.3).

Potassium and calcium. The availability of Ca^{2+} and K^+ generally increases in waterlogged soils (Ponnamperuma, 1984), but their uptake by intolerant species decreases with waterlogging (Kozlowski and Pallardy, 1984; and see Chapter 35). On the other hand, the most waterlogging-tolerant species in Schat's (1984) experiment showed no changes in uptake of these cations in waterlogged culture. This supports Kozlowski and Pallardy (1984) who assert that K^+ and Ca^{2+} absorption in waterlogged environments poses no problems for waterlogging-tolerant species. In periodically waterlogged saline environments, however, relatively high Na^+ concentrations pose problems for K^+ and Ca^{2+} uptake for herbs and grasses (Rozema, Luppens and Broekman, 1985a). In contrast, stimulation of potassium uptake by NaCl in waterlogging-tolerant mangrove species has been documented (Wainwright, 1984).

Other minerals and toxic effects. Aerenchymatous waterlogging-tolerant plants that are not waterlogged or are waterlogged less than is normal for that species have been reported to show signs of iron-deficient chlorosis (Eleuterius and Caldwell, 1981; Rozema, Bijwaard, Prast and Broekman, 1985b) through a mechanism discussed by Schat (1984). Zinc deficiencies can occur in rice paddy under certain conditions as discussed by Kozlowski and Pallardy (1984), and may limit anaerobic ethanol fermentation in roots (Moore and Patrick, in press).

Along with waterlogging, root discrimination regarding uptake of some minerals and compounds is often lost, leading to the accumulation of unwanted substances or toxic quantities of an essential element (Armstrong, 1975; Crawford, 1982a). This usually occurs in waterlogging-intolerant plants. For example, in comparative studies with wetland versus mesophytic species and ecotypes, essential elements and metals such as Fe, Mn, Mg, B and Li have been found to accumulate to toxic levels in the less waterlogging-tolerant plants (Jones and Etherington, 1970; Wu, 1981; Hodson, Smith, Wainwright and Opik, 1981; Rozema et al., 1985b). Recently, these findings have been extended to include distributional patterns across salt marshes (Rozema et al., 1985b). Similarly, species colonizing coastal mudflats without competition have been shown to overcome high concentrations of sulfide that

Table 34.4: Internal hormonal responses to hormone application or soil flooding of selected wetland plants and their effects on growth

Species	Treatment	Hormonal changes	Growth response	Reference
Rice	C_2H_4 applied to roots	Treatment	Root growth peaks at 1-10 ppm ethylene	Smith and Robertson (1971)
Rice	Flooding then draining	C_2H_4 increased	Stems elongated then lodged, reducing yield	Rose-John and Kende (1984)
<u>Callitrichia platycarpa</u>	Flooding	Stem C_2H_4 rises	Extension response saturated	Musgrave <i>et al.</i> (1972)
<u>Sagittaria pygmaea</u> <u>Potamogeton distinctus</u>	Flooding	Stem C_2H_4 rises	Extension response	Suge and Kusanagi (1985)
<u>Hydrocharis morsus-ranae</u> <u>Reineckia diphyllum</u> <u>Ranunculus sceleratus</u>	C_2H_4 and IAA applications to roots	Treatment	Extension growth from both hormones but by different mechanisms	Cookson and Osborne (1978)
<u>Ranunculus sceleratus</u>	C_2H_4 applied to root Petiole submergence	Treatment C_2H_4 increased	Extension growth Extension growth	Samarakoon and Horton (1984)
<u>Picea sitchensis</u> and <u>Pinus contorta</u>	C_2H_4 in hydroponics (28-110 ppm) 3 wks	Treatment	Growth reduced 40% at 28 ppm C_2H_4 trt	Sanderson and Armstrong (1980)
6 tree species	Flooding	C_2H_4 increased in all but least tolerant species	Greatest growth and survival in species producing the most adventitious roots	Sena Gomes and Kozlowski (1980a) Tang and Kozlowski (1984)

are toxic to their competitors (Ingold and Havill, 1984; Thibodeau and Nickerson, 1986).

Hormones

Hormonal responses to waterlogging are discussed in detail by Jackson (Chapter 31), and research demonstrating the link between hormonal response and growth in wetland species is summarized in Table 34.4.

Root Rhizosphere

Perhaps the most significant long-term adaptation of wetland species to soil waterlogging is the development of an internal gas path from the root to the shoot that assumes the external gas diffusion path once provided by the soil atmosphere (Hook and Scholtens, 1978; Armstrong, 1979). As well as providing for aerobic root respiration, the oxygen also diffuses out of the root into the surrounding soil, creating a microzone around the root termed the oxidized rhizosphere (Armstrong, 1979). This layer reverses many of the negative effects soil waterlogging has upon roots, from detoxifying reduced phytotoxins such as sulfides (Carlson, 1980; Thibodeau and Nickerson, 1986) to supplying mycorrhizal symbionts with oxygen (Read and Armstrong, 1972; Keeley, 1980).

Although few reports link a change in root rhizosphere with a growth response (Table 34.5), the development of aerenchymatous roots allows or enhances continued growth and survival of wetland plants during waterlogging episodes (Hook and Brown, 1973; Armstrong, 1979; Keeley 1979). In an experiment comparing waterlogging stress in two willow species that exhibit topographic zonation in a drainage basin subject to periodic long-term river flooding, the species that flourished in the lower areas was able to oxidize its rhizosphere to a greater extent (Dionigi, Mendelsohn and Sullivan, 1985). Similarly, Thibodeau and Nickerson (1986) showed that the distribution of two sympatric mangrove species depended upon their ability to oxidize the sediment around their roots (Table 34.5). Rhizosphere oxidation may also be obtained by plants growing in association with burrowing animals (Bertness, 1985) or with other plants that produce an extensive oxidized rhizosphere (Rozema et al., 1985a). Such associations with Juncus maritimus allowed increased root survival and shoot growth compared to similarly waterlogged plants in monoculture (Schat, 1984).

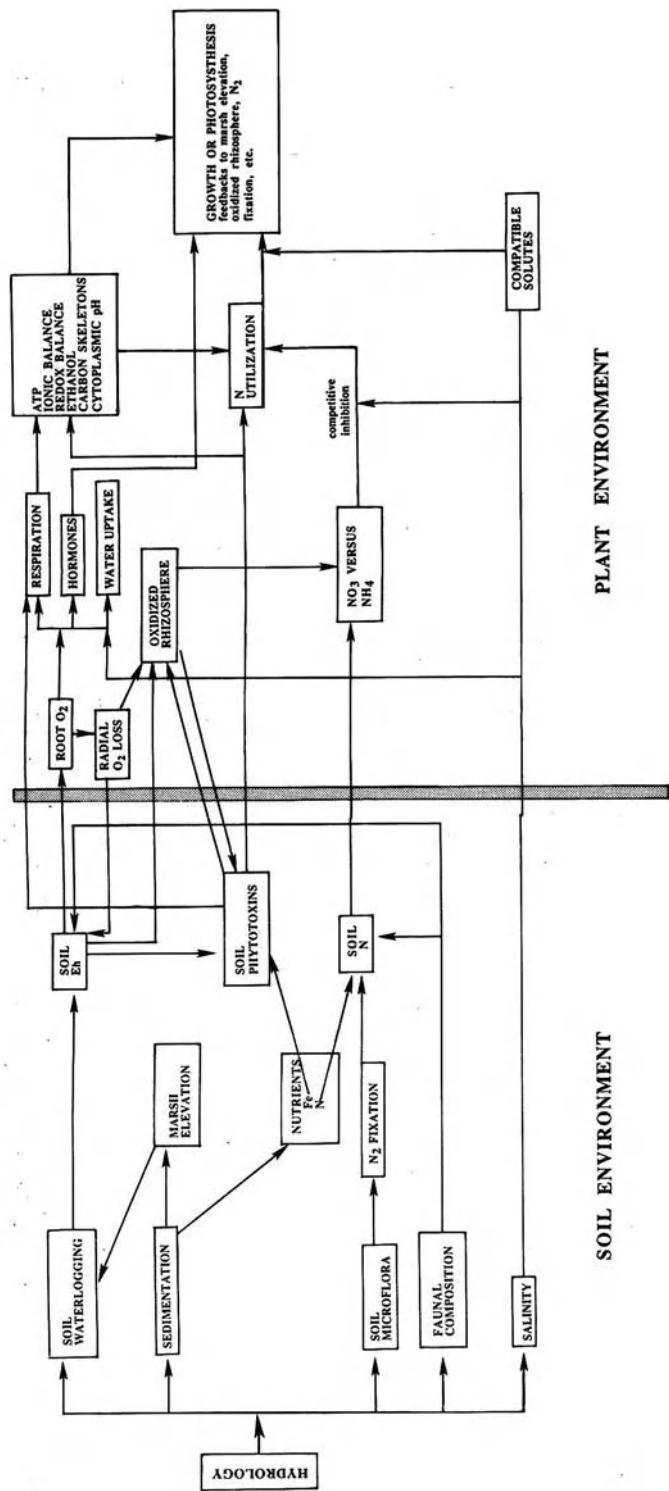
SOIL-ROOT-GROWTH INTERACTIONS IN *SPARTINA ALTERNIFLORA*

The relationship of hydrologically mediated soil parameters and root metabolism to primary production of Spartina alterniflora growing in regularly inundated salt marshes is described below (Figure 34.2). S. alterniflora was chosen because this species and its environment has been extensively investigated, and it is the

Table 34.5: Flooding effects on rhizosphere and associated growth responses in selected wetland plants

Species	Treatment	Changes in rhizosphere	Growth response	Reference
5 hardwood species	Seedlings flooded about 5 weeks	Oxidized by secondary roots of <u>Nyssa aquatica</u> only	Greatest growth in <u>Nyssa aquatica</u>	Hook and Brown (1973)
<u>Nyssa sylvatica</u>	Flooded 1 yr with mycorrhizal inoculum	Endomycorrhizal association	Increased growth	Keeley (1980)
4 dune slack species	Flooding with <u>Juncus</u> for 10 weeks	Oxygen persists in soil	Increased number of leaves, root and leaf survival	Schat (1984)
<u>Salix nigra</u> and <u>S.exigua</u>	Field: observation; Lab: flooding 7 wks	Unknown Eh fall less w/ <u>S.nigra</u>	<u>S.nigra</u> occupies lower sites. Leaf AEC drops in <u>S.exigua</u>	Dionigi et al. (1985)
<u>Spartina alterniflora</u>	In- and ex-closures to control <u>Uca</u> density	More burrows with greater density	Growth increases with <u>Uca</u> density	Bertness (1985)
<u>Avicennia germinans</u> and <u>Rizophora mangle</u>	S^{+2} and species distributions in field	More oxidized in <u>Avicennia</u> areas due to pneumatophores	<u>A.germinans</u> colonizes high S^{+2} areas but <u>R.mangle</u> cannot	Thibodeau and Nickerson (1986)

Figure 34.2: A conceptual model describing the interaction between soil and plant environments which influence productivity of *Spartina alterniflora*



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dominant salt marsh grass along the Atlantic and Gulf Coasts of the United States.

Soil Processes

Soil drainage. Although Spartina alterniflora salt marshes are flooded and drained on a daily basis, the degree of soil drainage that occurs during the ebb tide is not spatially constant throughout the salt marsh (Mendelsohn and Seneca, 1980; Howes, Howarth, Teal and Valielas, 1981; Agosta, 1985). The soil water-table at low tide is seldom below the soil surface within the less productive inland Spartina zones, but may fall 20 cm or more within the more productive marsh zones adjacent to tidal creeks (Howes et al., 1981; Mendelsohn, McKee and Postek, 1982). This differential soil drainage results in significant differences in soil redox potential with the more waterlogged sites having the more reduced soil conditions (Howes et al., 1981; Mendelsohn et al., 1982; Delaune, Smith and Patrick, 1983) and the less productive S. alterniflora (Linthurst and Seneca, 1980; Mendelsohn and Seneca, 1980). Manipulative field (Mendelsohn and Seneca, 1980; Wiegert, Chalmers and Randerson, 1983) and greenhouse (Linthurst and Seneca, 1981) experiments have demonstrated that prolonged soil waterlogging detrimentally affects the growth of this species.

Soil phytotoxin accumulation. In salt marsh systems dominated by Spartina alterniflora H_2S has received the most attention of the phytotoxic substances that accumulate in waterlogged soils. Sulfide accumulates to concentrations of 1-5 mM or more in the more waterlogged areas of the marsh (Carlson and Forrest, 1982, Howes, Dacey and Wakeham, 1985). In a Louisiana salt marsh, Delaune et al. (1983) correlated higher marsh elevations with lower soil sulfide concentrations. King, Klug, Wiegert and Chalmers (1982) found in a Georgia salt marsh that, in addition to soil waterlogging, the input of dissolved iron had a significant affect on interstitial sulfide concentration. By artificially increasing the degree of soil water movement into a more waterlogged zone of the salt marsh, these researchers increased the concentration of dissolved iron which precipitated H_2S as FeS and thereby reduced the free sulfide concentrations in the interstitial water. Impairing soil drainage had the exact opposite effect, i.e. dissolved iron decreased and H_2S increased. In a companion study, Wiegert et al. (1983) demonstrated that this increased soil water movement significantly stimulated plant growth.

The sulfide that accumulates in the more waterlogged zones of the salt marsh is taken up by Spartina alterniflora (Carlson and Forrest, 1982; Fry, Scalan, Winters and Parker, 1982). Since H_2S is potentially toxic to higher plants (Allam and Hollis, 1972; Joshi, Ibrahim and Hollis, 1975; Gambrell and Patrick, 1978), the question arises as to whether sulfide decreases the growth of Spartina alterniflora. Although no published experiments have been conducted to determine directly the effect of H_2S on growth in S.

alterniflora, information available for other salt marsh species indicate that sulfide can reduce nutrient uptake, root respiration, and inhibit important enzyme activity (Havill et al., 1985). Goodman and Williams (1961) demonstrated that soft-rotting of S. townsendii rhizomes occurred when concentrations of 1 mM sulfide were added to solution culture. Correlative investigations with S. alterniflora suggest reduced growth at sulfide concentrations above 1 mM (Peterson and Howarth, unpublished manuscript; Mendelsohn and McKee, unpublished data). Morris (1980) and Mendelsohn and Seneca (1980) have suggested that sulfide or some other factor associated with soil waterlogging may inhibit ammonium uptake in S. alterniflora and as a result limit growth. In fact, the more inland or short form of S. alterniflora which often inhabits the more waterlogged and sulfide-rich zones of the marsh is nitrogen limited (Mendelsohn, 1979a,b). However, the inhibition of ammonium uptake by sulfide has yet to be demonstrated in S. alterniflora, although this inhibition does occur in rice (Okajima and Takagi, 1953).

As mentioned earlier, substances other than H₂S can be phytotoxic under waterlogged conditions. Iron and manganese have been given some attention for certain wetland vegetation (Cooper, 1982, 1984; Singer and Havill, 1985; Rozema et al., 1985), although the effects of these two elements on the growth of S. alterniflora is less well understood (Adams, 1963; Broome, Woodhouse and Seneca, 1975; Roberts, 1976; Haines and Dunn, 1976). The influence of other substances that accumulate in waterlogged soils have not been investigated.

Marsh sedimentation. The rate of marsh sedimentation is a direct function of hydrology (Stumpf, 1983) and influences the growth of S. alterniflora. Baumann, Day and Miller (1985) demonstrated that the more productive streamside S. alterniflora marshes in Louisiana vertically accrete at a rate (approximately equal to the apparent rise in sea level) faster than the low productivity inland marshes. Thus the inland marshes cannot keep pace with increasing water levels and eventually become too waterlogged to survive, resulting in Spartina die-back. The sediment that vertically accretes the marsh also provides nutrients to the vegetation, and encourages underground production which also contributes to the vertical marsh accretion (Hatton, Patrick and DeLaune, 1982; Hatton, DeLaune and Patrick, 1983).

Nitrogen cycling. Differential hydrology also influences soil processes important in nitrogen cycling such as nitrogen fixation. Ubben and Hanson (1980) found a direct relationship between nitrogen fixation potential, determined by the acetylene reduction technique, and daily tidal inundation. In a Georgia salt marsh, the highest rates of nitrogen fixation were associated with those marsh sites adjacent to tidal creeks where tidal inundation and soil drainage of pore water occur daily. Interstitial salinity was not correlated with nitrogen fixation potential. The nitrification and

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denitrification processes are also influenced by hydrology (Gambrell and Patrick, 1978).

Salinity. The influence of hydrology in controlling salinity concentrations in the salt marsh is another important hydrology-soil response. Salt concentrations can increase in the high or irregularly flooded marsh as evaporation concentrates the salt that is introduced by tidal inundations. Since tidal input to the high marsh is irregular, leaching and dilution of this accumulated salt occurs infrequently, and as a result, hypersaline conditions can occur. Cavalieri and Huang (1979) demonstrated that high salt levels stimulate the synthesis of nitrogen-containing solutes (proline and glycine betaine) in Spartina alterniflora. These solutes are thought to aid the plant in salt tolerance. However, they represent a drain on the nitrogen that would normally be used in growth (Cavalieri and Huang, 1981). At high salinities, photosynthesis by S. alterniflora decreased due to a direct effect on metabolic processes as well as increased leaf stomatal resistance (Durr, Haines and Giurgevich, unpublished manuscript). Salt can also affect growth through the action of sodium as a competitive inhibitor of ammonium uptake (Haines and Dunn, 1976).

Faunal composition. Hydrology can also affect the faunal composition of the salt marsh which in turn can influence nitrogen and soil redox potential (Eh). Bertness (1984) demonstrated via manipulative field experiments that the ribbed mussel, Geukensia demissa, stimulates the growth of S. alterniflora through a nitrogen fertilization effect from the mussels' feces and pseudofeces. Bertness (1985) also found that fiddler crabs, Uca pugnax, through their burrowing activity increased the percolation rate of water through the sediment, allowing for greater soil water drainage and air entry into the sediment, and greater plant growth. Hence, invertebrate populations in the marsh appear to be important controllers of plant productivity.

Root Process

Oxygen transport and oxidized rhizosphere. The extent of inundation and soil waterlogging can affect oxygen transport to the root and the development of an oxidized rhizosphere. Spartina alterniflora has a well-developed aerenchyma system that allows for O₂ transport from the atmosphere through the plant and to the soil environment. Oxygen transport rates in S. alterniflora have been estimated at between 1.4 and 3.8 $\mu\text{l min}^{-1}$ (Morris and Dacey, 1984). This transport is evidenced by the Fe precipitation found around the root (Mendelssohn and Postek, 1982).

Oxygen transport in S. alterniflora is affected by tidal level and light (Gleason and Zieman, 1981). At a constant illumination, O₂ concentration in the shoot base decreases with increasing tide height. Movement from light to dark results in the O₂ concentration decreasing even when water level is falling. Gleason and

Zieman (1981) concluded that photosynthetic O₂ production significantly contributes to the internal O₂ supply of this plant and that plant submergence reduces internal oxygen supply. Hence, when tidal submergence coincides with the evening period, internal root oxygen supply may be greatly reduced.

The O₂ that diffuses from the roots can create an oxidized rhizosphere that buffers the plant against soil toxins like H₂S. For example, Carlson (1980) demonstrated that root-induced decreases in sulfide concentration, presumably due to root oxidation, occurred during periods when *S. alterniflora* was exposed to the light; sulfide increased during the dark periods. The oxidized rhizosphere of the more productive streamside *S. alterniflora* appears to be better developed than that of the low vigor inland swards (Mendelsohn and Postek, 1982).

Root respiration. Degree of soil waterlogging may also affect root respiration and the extent of anaerobic metabolism. Even in a plant with an extensive aerenchyma system like *S. alterniflora*, O₂ deficiencies may result under extreme waterlogging (Mendelsohn et al., 1981). Mendelsohn and McKee (1986) demonstrated that a hypoxic root environment can stimulate root alcohol dehydrogenase (ADH) activity (an indicator of the capacity for alcoholic fermentation) in *S. alterniflora*. In the field, *Spartina* in the more waterlogged zones of the marsh exhibited greater root ADH activity than that in the less waterlogged areas (Mendelsohn et al., 1981). Furthermore, the transplantation of swards of streamside *S. alterniflora* into the more waterlogged inland zone caused a significant increase in ADH activity, whereas the transplantation of inland swards into the less waterlogged streamside zone resulted in a significant decrease in ADH activity (McKee and Mendelsohn, unpublished data). These data indicate that increased waterlogging and subsequent root hypoxia cause a reduction in aerobic respiration and a stimulation of the capacity for alcoholic fermentation. Supporting this conclusion, Morris and Dacey (1984) found a decrease in aerobic respiration, measured as O₂ uptake by the root, in *S. alterniflora* at O₂ concentrations between 3 and 5 per cent. Oxygen concentrations above 5 per cent resulted in maximum respiration rates. Hence, it would appear that reduced aerobic respiration and increased anaerobic metabolism in the roots of *S. alterniflora* is a probable consequence of highly reduced soil conditions.

Metabolic consequences of anaerobic root metabolism. The change from aerobic to anaerobic root metabolism may cause certain metabolic problems including an energy (ATP) deficiency, ethanol toxicity, carbon loss, and/or an inability to maintain cytoplasmic pH, redox status and ionic balance (Crawford, 1978; Roberts et al., 1984b).

Waterlogged conditions do not appear to cause a root energy deficiency for *S. alterniflora* as long as alcoholic fermentation is induced. Mendelsohn et al. (1981) found that the root AEC of *S. alterniflora* in the most chemically reduced zone of the salt marsh

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(where ADH activity was stimulated) was as high as that of plants growing in the least reduced areas. However, ADH activity decreased within the die-back zone of the marsh and the AEC decreased concurrently. In the greenhouse, hypoxic root environments resulted in equal or greater root AECs than under drained or aerobic conditions (Mendelssohn and McKee, 1986). Under hypoxia, the AEC of S. alterniflora roots appears to be related to root ADH activity, which in turn increases as the soil becomes more reduced (Mendelssohn and McKee, 1986). These preliminary data support the findings of Saglio et al., (1983) that the AEC can be maintained at relatively high levels under hypoxia as long as alcoholic fermentation is stimulated.

The ability to maintain a high AEC under hypoxia may be dependent on an increased consumption of glucose or on a decreased utilization of ATP. If the increased consumption of glucose is a result of increased alcoholic fermentation, ethanol may increase to high levels in the roots. Although the question of ethanol toxicity in root tissue is still a debatable point (Jackson et al., 1982), ethanol appears to diffuse readily from S. alterniflora roots (Mendelssohn et al., 1981; Mendelssohn and McKee, 1986) thereby avoiding potential toxicity. This leakage, however, may be a significant carbon drain to the plant, especially if glucose consumption is simultaneously stimulated. A deficiency of carbon skeletons available for nitrogen metabolism could result in reduced nitrogen utilization and reduced growth (Michael, Martin and Owassia, 1970). The extent to which a root carbon deficiency under hypoxia inhibits the growth of S. alterniflora needs further attention. The extent that hypoxia interferes with the maintenance of cytoplasmic pH, redox status and ionic balance has not been investigated in S. alterniflora.

Nitrogen uptake. Although no one has shown that increased anaerobic metabolism in S. alterniflora reduces growth, Morris and Dacey (1984) have demonstrated that ammonium uptake is reduced at low root oxygen concentrations, approximately the same concentrations at which aerobic respiration is inhibited. Hence, growth could be detrimentally affected by this decrease in nitrogen uptake. However, DeLaune et al., (1984) found no inhibition of $^{15}\text{NH}_4^+$ uptake in S. alterniflora at low redox potentials where O_2 should have been completely absent from the root culture. These contradictory data concerning the effect of low O_2 conditions on ammonium uptake in S. alterniflora need to be resolved. Salt water inundation can also have an effect on nitrogen uptake as discussed by Haines and Dunn (1976). Parrondo, Gosselink and Hopkinson (1981) showed that the uptake of the monovalent cation Rb was inhibited by salt (Na) in S. alterniflora.

There is no evidence that inundation with freshwater affects water uptake in this species. However, inundation with salt water does decrease the osmotic potential of the leaf but not enough to maintain turgor pressure (Drake and Gallagher, 1984); thus cell expansion and growth could be reduced.

Summary

The interaction of hydrologically mediated soil phenomena and root processes are intimately linked to control the growth of S. alterniflora. Water movement through the marsh substrate is essential in providing Fe to the system and increasing soil aeration, both factors which lower H₂S concentrations. Spartina alterniflora growing in the more aerated zones of the marsh exhibit less anaerobic root metabolism and are less nitrogen deficient than individuals of this species in the more flooded zones. The absence of high levels of H₂S and of anaerobic root metabolism in the better-aerated substrate allows for adequate nitrogen utilization in addition to providing better sites for nitrogen fixation and mineralization. Invertebrates, dependent upon marsh hydrology, appear to play a significant role in adding nitrogen (mussel) and aerating the substrate (fiddler crab), factors which can positively influence nitrogen availability and utilization by Spartina alterniflora.

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Chapter Thirty-five

MINERAL NUTRITION OF OXYGEN-STRESSED CROPS AND ITS RELATIONSHIP TO SOME PHYSIOLOGICAL RESPONSES

R.E. Sojka and L.H. Stolzy

Historically nutritional studies of anoxic plants have simply catalogued concentration and uptake changes of treated plants, frequently on a non-partitioned whole-plant basis. Major reviews of soil aeration and flooding generally agree that N, P, and K concentrations in plants are reduced by anoxia (Kozlowski, 1984; Glinski and Stepniewski, 1985). Sodium concentration increases and other major elements either remain unaffected or react irregularly. Until recent years explanations of nutritional changes have focused chiefly on alterations in the poorly aerated soil physicochemical environment. Factors such as: increased mineral solubilization, leaching, and dilution in high water content soils, increased water film coverage of roots, altered ion diffusion, solubility changes at altered valence states, altered pH resulting from redox reactions or increased CO₂ concentrations, etc. have been used to explain nutritional responses to oxygen-limiting soil environments.

Sojka and Busscher (1986) have recently compiled an extensive plant/soil-aeration bibliography. Since the mid 1970s there has been an increase in papers relating changes in plant nutrient contents to interactions between the environment and plant physiological processes.

Farmers and many scientists (Arnon, 1937; Gilbert and Shive, 1942; Malvolta, 1954; Willhite, Grable and Rouse, 1965) have long believed that high nitrate concentrations reduce crop susceptibility to flooding. Upon flooding the falling E_h poises briefly along a series of plateaus as the soil depletes each pool of successively less-willing electron acceptors (Patrick and Mikkelsen, 1971; Russell, 1976). Garcia-Novo and Crawford (1973) concluded that a species' flood tolerance is related to effective use of nitrate as an alternative electron acceptor during anaerobiosis. Lotocki (1977) found that Scots pine (Pinus silvestris L.) seedlings supplied with sodium nitrate or ammonium nitrate grew better during flooding than seedlings supplied with ammonium chloride. Mixtures of ammonium and nitrate as N sources performed intermediate.

In flooded soils leaching, denitrification by micro-organisms, and volatilization occur. At least some of the decline in plant nitrogen under these conditions is probably attributable to reduced availability (Singh and Ghildyal, 1980). Few of the aeration x nutrition studies reported have been conducted in anything approaching aseptic conditions. The effects of an interacting

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microbial ecology on the root mass has not been thoroughly evaluated with respect to its effect on mineral nutrition under poorly aerated conditions. In one study (Trolldenier and von Rheinbaben, 1981) combined root/microbial respiration of wheat (*Triticum aestivum* L.) was lowest when using NO_3^- as the N source and highest with NH_4^+ as the N source. Intermediate results were obtained for mixtures. Furthermore, whereas discontinuation of K in the nutrient solutions did not affect solely nitrate-fed plants, respiration increased with $\text{NO}_3^-/\text{NH}_4^+$ mixtures and decreased with solely ammonium-fed plants when K was removed.

Reduced growth of wheat and barley (*Hordeum vulgare* L.) is more closely related to the drop in O_2 availability than to available nitrogen concentrations in flooded soils (Drew and Lynch, 1980; Trought and Drew, 1980a; Drew and Sisworo, 1977, 1979). When either NO_3^- or NH_4^+ ions were added to the aerobic soil surface or when urea was sprayed on foliar parts, chlorosis and N deficiencies associated with early stress-induced senescence of tops was prevented (Trought and Drew, 1980b). Uptake of P and K was also similarly affected by the treatments (Trought and Drew, 1980c; Drew, Jackson and Gifford, 1979).

Perhaps the most significant finding in the Letcombe experiments is the fate of plant nutrients after cessation of root uptake. Nutrients were quickly mobilized away from mature tissue to satisfy nutrient sinks in immature expanding tissue in both barley (Drew and Sisworo, 1977, 1979) and wheat (Trought and Drew, 1980b). This response was similar for N, P, and K. Earlier, Leyshon and Sheard (1974) had found that flooding effects on these nutrients were more profound in younger than mature plants. Young plants have no pool in mature tissues of easily remobilized nutrients. Also important in these studies was the rapidity of events. Root nutrient uptake halted immediately with loss of adequate root aeration, and significant nutrient redistribution was measurable in 24 to 48 h. Such time-course responses make it reasonable to consider the involvement of altered mineral-nutrition of anaerobic plants in some conspicuous physiological reactions. A good example is stomatal response to aeration.

Stomatal response is highly dynamic, responding to a variety of direct and indirect environmental stimuli. Evidence for a link between potassium nutrition and stomatal regulation has been accumulating for 80 years (McCallum, 1905; Snow, 1936). Potassium ion flux into and out of guard cells has been identified as the specific mechanism affecting guard cell turgor and hence stomatal aperture (Fujino, 1959; Fischer, 1968). It has been demonstrated that alteration of whole-plant K nutrition affects stomatal behavior (Graham and Ulrich, 1972; Wardle and Simpkins, 1979; Cooper, Blaser and Brown, 1967; Peaslee and Moss, 1966). Perhaps the most consistent nutritional response to root anoxia is reduced K uptake and plant K^+ concentration. Hammond, Alloway and Loomis (1955) reported an approximately linear relationship between water use and K absorption from the nutrient solution by corn plants grown under varying root oxygen regimes. Moldau (1973) and Regehr, Bazzaz and Boggess (1975) reported decreased stomatal conductance to water vapor for bean leaves (*Phaseolus vulgaris* L.) under flooding equivalent to conductances seen in drought.

Moldau termed this condition 'physiological (as opposed to physical) drought.' The direct linkage of this phenomenon to oxygen removal from roots was subsequently determined for wheat (Sojka, Stolzy and Kaufmann, 1975). In a later paper Sojka and Stolzy (1980) showed that a stomatal response-threshold of $20 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$ ODR (soil oxygen diffusion rate) existed for several species studied. Plant analysis showed reduced K concentrations at the lower ODRs as well. The authors hypothesized that reduced K concentrations could interfere with normal maintenance of guard cell turgor under anoxic conditions. Decreased leaf conductance and lower K concentrations were found in a field study (Meek, Owen-Bartlett, Stolzy and Labanauskas, 1980) with cotton (Gossypium hirsutum L.) when water-tables were kept above 30 cm in depth.

In a recent experiment Sojka (1985) determined that the threshold ODR for soybean (Glycine max) is $40 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$ and that 48 h exposure to the threshold ODR was necessary to induce closure. Leaf K, Ca, and Mg were monitored in several harvests in an attempt to link K concentration changes to stomatal performance. Whole-plant tissue analyses were confounded late in the experiment and it was speculated that because significant lower leaf drop occurred, there was translocation to remaining juvenile leaves, above the position of stomatal monitoring. Although declining uptake and reduced K concentrations followed familiar trends with exposure to reduced oxygen the direct link to stomatal activity remained inconclusive. It was noted, however, that change in growth and nutrient concentrations began in the experiment at ODR thresholds less severe than that for stomatal closure, leading to the conclusion that individual physiological responses probably each have their own unique response thresholds. Peoples and Koch (1979) had earlier found that RuBPC (ribulose-1,3-bisphosphate carboxylase) synthesis, and photorespiration rates of alfalfa declined with mild K deficiency, but that stomatal closure did not occur until the deficiency became more severe. It is likely that numerous responses to reduced ODR occur in this fashion on a continuous scale of interacting primary and secondary stimuli.

Concentrations and morphological distribution of numerous hormones and their precursors including ethylene, ACC (1-amino-cyclopropane-1-carboxylic acid), CK (cytokinin), GA (gibberellins), ABA (abscisic acid), and others are drastically altered with flooding or reduced ODR (Reid and Bradford, 1984). The pervasive involvement of ethylene in flooding response, particularly in bringing about leaf epinasty coupled with the ease of its analysis led to much early speculation regarding its direct involvement in stomatal closure. Several experiments, however, would seem to indicate otherwise (Pallaghy and Raschke, 1972; Bradford, 1982, 1983; El-Beltagy and Hall, 1974; Bradford and Yang, 1981). These and other studies (Wright, 1972; Pierce and Raschke, 1980; Sivakumaran and Hall, 1978; Shaybany and Martin, 1977; Hall, Kapuya, Sirakumaran and John, 1977) have shifted interest to the role of ABA (abscisic acid) as the hormonal trigger of stomatal response during flooding. Its implication seems certain, and is consistent with the involvement of ABA in stomatal closure from drought stress (Jones and Mansfield, 1972; Hiron and Wright,

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1973; Wright, 1977). It has been shown (Jones and Mansfield, 1970) that ABA acts directly on stomatal control by impairing guard cell ability to accumulate and/or retain potassium ions (Mansfield and Jones, 1971) and by causing a transient potassium and chloride ion efflux (MacRobbie, 1981).

As stated earlier, N-deficiency, like K-deficiency, is common in leaves of poorly aerated plants. A recent series of cotton (Gossypium hirsutum) experiments on the interaction of N-deficiency and drought in cotton (Radin and Parker, 1979; Radin and Ackerson, 1981; Radin, 1981; Radin, Parker and Guinn, 1982) produced results relevant to flood-induced stomatal closure. In these studies increased endogenous ABA content was found at high plant water potentials (ψ_p) in N-deficient plants resulting in greater stomatal sensitivity to stress. The effects of N-supply on stomata could not be explained by passive linkage to ψ_p . Stomatal closure occurred at higher ψ_p in N-deficient plants than in normal plants. A similar independence from ψ_p of stomatal response during root anoxia was reported by Sojka and Stolzy (1980). In another series of cotton experiments (Reicosky, Meyer, Schasfes and Sides, 1985a; Reicosky, Smith and Meyer, 1985b; Hocking, Reicosky and Meyer, 1985) N and K levels declined in leaves following flooding. The drop in N best explained growth reductions and was also associated with increased foliage temperature and reduced photosynthesis. The latter two responses implicated stomatal closure, but that parameter was not directly observed.

Another interesting physiological response to root zone anoxia is root porosity or so-called aerenchyma tissue formation. The existence of root porosity has been known for many years (Dunn, 1921; McPherson, 1939). The topic was reviewed by Luxmoore, Sojka and Stolzy (1972). They conceived of a metabolically driven conceptual model in which high light intensity (because of its promotion of rapid growth) or oxygen shortage (relative to respiratory demand) could individually or interactively promote root air-space formation. Aerenchyma formation is widely believed an evolutionary adaptive response to low-oxygen root environments which allows increased internal O₂ diffusion to oxygen-stressed roots, thereby enabling continued aerobic respiration. Even in the new mass flow theory of O₂ to submerged rice (Oryza sativa) roots (Raskin and Kende, 1983, 1985), formation of high porosity favors survival due to the reduction in pathway resistance.

Interplay of mineral nutrition as a root air space formation factor has gone largely uninvestigated. A few recent reports, however, suggest that mineral nutrition may be an important consideration. Konings and Verschuren (1980) reported a relationship between a decline in nutrient solution N (as NO₃⁻ or as NH₄⁺) and increased root air-space development. They explained the promotion of root porosity observed by Luxmoore *et al.* (1972) during high light intensity periods or elevated temperature on the basis of a NO₃⁻ shortage in the roots during a period of high assimilatory demand. Hardcastle and Schutte (1983) found that if maize (Zea mays) roots were grown either in anaerobic solutions or in solutions deficient in nitrate and phosphate that root porosity increased. Furthermore, they observed that air-space formation in

nutrient-deficient solutions was more severe when the solutions were anaerobic.

The issue appears to be more complicated, however, with ethylene playing a role in maize root aerenchyma formation as well (Drew, Sisworo and Sakes, 1979; Drew, Jackson, Gifford and Campbell, 1981; Konings, 1982). Nutrient levels were never limiting in these studies, and thus the influence of N metabolism in mediating the ethylene response remains undefined. Jackson, Fenning and Jenkins (1985) found no ethylene influence on aerenchyma formation in rice and that its development proceeded regardless of O₂ status. Others have observed greater root porosity development in rice at low O₂ partial pressure (Armstrong, 1971; Das and Jat, 1977). Konings and de Wolf (1984) found that other growth-regulating substances affected aerenchyma formation on non-aerated or NO₃⁻-starved roots as well, but that their action did not occur through mediation of ethylene.

A particularly interesting aspect of the work by Drew et al. (1979) was that while very low O₂ levels stimulated ethylene production and root aerenchyma formation, both were halted by absolute removal of O₂. Phosphorus has not been studied separately in relation to aerenchyma formation but Jackson, Drew and Gifford (1981) showed that ethylene exposure contributed to reduced phosphorus uptake in roots similar to flooding, but without an effect on N or K. It seems that while ethylene may be active in root porosity induction its production and activation may require the gradual reduction of O₂, possibly allowing a precursor such as ACC to be produced. Aeration-induced nutritional deficiency may be involved as an added stress signal inducing ethylene production. In the transition environment between drained and inundated soil these factors may come together synergistically. Interestingly, it has been reported that ABA, which is linked to stomatal closure of flooded plants, is a naturally occurring inhibitor of aerenchyma formation (Konings and de Wolf, 1984).

Another root response affected by flooding is geotropism. Root penetration decreases into waterlogged or otherwise poorly aerated horizons and roots may follow shallower angles or even grow above the anoxic zone at the interface of the adequately aerated surface soil (Ycas and Zobel, 1983; Wiersum, 1979; Papenhuijzen, 1979; Nazrul Islam, Saha and Khan, 1980; Jackson, 1985). A report by Bejaoui (1980) indicated an interaction of sodium ion and oxygen uptake in this phenomenon. In his work 50 mM NaCl in addition to inhibiting growth and oxygen uptake by roots, increased their geotropic sensitivity with the effect more pronounced in lateral roots. Sodium concentration is commonly observed to increase in oxygen-stressed plants (Labanauskas et al., 1966, 1971, 1972, 1975; Leggett and Stolzy, 1961; Pessoa da Costa and Smucker, 1981; Letey et al., 1961, 1962, 1965; Drew and Dikumwin, 1985; Drew and Läuchli, 1985). Anaerobic Na uptake is a metabolically coupled process (Leggett and Stolzy, 1961). In their work, Na uptake by roots of anaerobic plants decreased with time indicating that some process was 'attenuating'. They interpreted this to show that Na uptake was metabolically driven but several steps removed from the respiratory process. In an anoxic pretreatment, anaerobiosis per se did not activate Na

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uptake in shoots, instead it increased the Na uptake rate on returning to aerobic conditions. Root and shoot uptake appeared to involve separate processes. The effects of low soil O₂ and root Na uptake may act to counter one another. The geotropic stimulus of Na may dampen the apparently hormonally induced lateral stimulus of root growth or may reinitiate geotropic response when the soil profile drains.

Various attempts have been made to nutritionally ameliorate anaerobic (usually flooded) soils (Karlen, Sojka and Robbins, 1983; Ponnamperuma, Yuan and Nhung, 1965; Trought and Drew, 1980, 1981; Drew *et al.*, 1979; McKee, Hook, DeBell and Askew, 1984; Bryce, Focht and Stolzy, 1982; Herr and Jarrell, 1980; Hodgson, 1982; Magunda, Callebaut, DeBoot and Gabriels, 1984). These efforts have usually been aimed at N involvement in the anaerobic metabolism (as discussed earlier), at combatting specific nutrient deficiencies in flooded soils, or at providing so-called 'oxygen fertilizers' to ameliorate directly the soil redox status. In both of the two latter approaches the success has depended somewhat on flooding duration at time of treatment, method, and amount of application and plant growth stage. Oxygen fertilization, while promising in some instances, is expensive and may not be practical on a field scale for all but high value crops or ornamentals or in glasshouse operations. The effectiveness of all the approaches is very much affected by the severity of the anoxic regime being combatted.

CONCLUSION

This review has not been all-inclusive, but illustrates application of concepts of mineral nutrition to the understanding and improved management of crop growth under anaerobic conditions.

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Chapter Thirty-six

RESPONSES OF WOODY SEEDLINGS TO ELEVATED FLOOD WATER TEMPERATURES

Kenneth W. McLeod, Lisa A. Donovan and Nancy J. Stumpff

Multiple stresses acting simultaneously may affect plants more, the same, or less than each would individually. With the large number of environmental stresses created by man's activities, determining the effects of a single stress is exceptionally difficult. A single stress (e.g. flooding, high temperature, chemical addition, etc.) usually affects many aspects of the physical environment, producing both positive and negative results. Determining these effects as well as the interactions of several stresses is usually required to achieve a predictive capacity for multiple stresses. Hence, the individual effects of flooding and high substrate temperature will be briefly reviewed, after which their combined effect on the growth, morphology and physiology of woody seedlings will be discussed.

FLOOD STRESS

The terms flooded, saturated and waterlogged soil indicate differences in the amount of standing water present, but refer to similar soil environments. Changes that occur following flooding include reduced O₂ and increased CO₂ content of the soil (Armstrong, 1975). The rapidity of these changes depends on biological activity (root and microbial) in the soil and on diffusion of gases through the water column and the soil. Diffusion is usually slow, but varies with water depth, temperature, and turbulence. When oxygen is limited, Fe and Mn are converted into their reduced forms. Biota may modify this anoxic soil condition over the long-term but their impact is small in the short-term. Thus, soon after flooding, plant roots are subjected to anoxic conditions. However, flooding affects the whole plant, not simply the root system directly exposed to the stress. Indirect effects on the aerial portions of the plant are expressed through changes in water transport, hormone production and other root-controlled processes.

Stresses such as flooding change the abiotic environment over both spatial and temporal scales. Plants respond physiologically to the stress, but the response depends on whether the species is capable of surviving short, moderate, or long-term waterlogging. Some species are evolutionarily adapted to withstand long-term flooding by tolerating and/or avoiding the stressful condition,

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following morphological and/or physiological acclimation. Adaptations which permit tolerance to flooding include the maintenance of metabolic control and tolerance to both soil toxins and anaerobic respiration end-products (ethanol, lactic acid, malate, etc.) that may accumulate in the root tissue. This tolerance, in itself, may or may not impart long-term survival value, but does allow the plant additional time to acclimate to the newly flooded, anoxic root environment. Some researchers believe tolerance is an integral part of the overall adaptive mechanism and functions in concert with avoidance mechanisms, while others believe tolerance to be of value only over the short term.

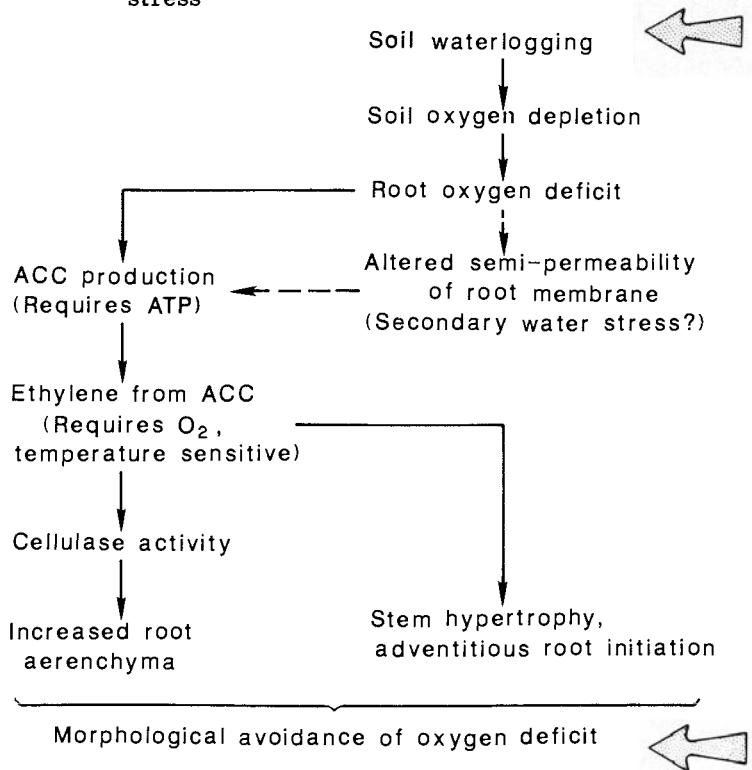
Species may also adapt through development of avoidance characteristics which facilitate oxygen transport within the plant from aerial portions to the submerged root system. These include increased aerenchyma formation, stem hypertrophy, lenticel production and hypertrophy, adventitious root production and soil water root production. Excellent reviews of plant adaptation and acclimation to flooding stress are found in Crawford (1982) and Hook (1984a). The processes controlling morphological acclimation are not fully understood, but are correlated with increased ethylene production and cellulase activity (Kawase, 1981; Figure 36.1).

During this acclimation process, basic root physiology proceeds in an anaerobic environment created by flooding. As soil waterlogging persists and acclimation proceeds, aerobic metabolism in the plant roots depends on oxygen supplied through the internal aeration system. This supply may be more than adequate, as evidenced by the radial oxygen loss from roots of some species (Armstrong, 1975). Acclimation continues until the stress is alleviated, but resumes with its re-occurrence.

TEMPERATURE STRESS

Research concerning the effects of high atmospheric temperature is abundant in the literature, but high substrate temperature has been primarily studied relative to agricultural (Nielson, 1974) and desert plants (Kappen, 1981); neither of which is generally confronted with flooded habitats. In most of these studies, the entire plant is exposed to the effects of high temperature. Agricultural experiments involved with high soil temperature are primarily concerned with the Q_{10} effect and mortality caused by extreme temperature conditions. Whether plants can become acclimated to high soil temperatures is unknown, although there is evidence for either acclimation or thermal optima at high air temperatures, especially regarding the C4 photosynthetic pathway (Kappen 1981). An interesting result of research on the effects of high soil temperature on apple trees (Gur, Bravdo and Mizrahi, 1972) was that acetaldehyde and ethanol were found in the roots of high-temperature treatments, indicating that anaerobic metabolism occurred. Gur et al. indicated that high temperature accelerated respiration to the point that the roots experienced anaerobic conditions. They also observed increased temperature and resistance of the leaves with decreased transpiration, due to the 35°C soil temperature.

Figure 36.1: Schematic of the development of morphological acclimation characteristics in response to flooding stress



ELEVATED TEMPERATURE/FLOOD STRESS

Little research has been conducted on the multiple stress of flooding by high temperature water. Release of thermal effluents from nuclear production reactors has inundated sections of the Savannah River swamp forest, resulting in tree mortality and shifts in community composition (Sharitz, Irwin and Christy, 1974). The combination of high-temperature water and flooded conditions is not unique to man-altered environments. Shallow pools on floodplains, occasional standing water associated with high rainfall or poor drainage and shallow ponds can all be subjected to intense solar heating. In Carolina bays (shallow rainfed ponds that are unique to the coastal plain of the southeastern United States), water temperatures have been observed as high as 37°C. Since this multiple stress is found in natural environments, biota have been exposed to its selective pressure over evolutionary time.

The effects of high-temperature flood stress on bald cypress (*Taxodium distichum* (L.) Richard) and water tupelo (*Nyssa aquatica* L.), the former dominants of the Savannah River swamp

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forest, and black willow (*Salix nigra* Marshall) and button bush (*Cephalanthus occidentalis* L.), colonizers of the stressed habitat (Sharitz et al., 1974), were studied. The experimental approach in these studies has been to impose controlled conditions, manipulating the flood magnitude and water temperature, on potted seedlings of these four species.

In a large microcosm experiment, seedlings were grown for one year in continuous soil moisture conditions that ranged from unsaturated (DR) to 6 cm of standing water (FL), and in water temperatures of ambient (~30°C maximum (LW)), ambient + 5°C (MD), and ambient + 10°C (HG) (see Donovan, McLeod, Sherrod and Stumpff (submitted) for details). All four species are flood tolerant (Hook, 1984b) and should have had time to acclimate to the stressful environment within the experimental period. Two comparisons among treatments will be considered: (1) do differences exist between seedlings in unsaturated and flooded treatments in the ambient temperature? and (2) do elevated temperatures cause differences in plant response within the flooded treatments?

Survival of the four species over one growing season was not affected by ambient-temperature continuous flooding, but it was reduced by continuous flooding with ~40°C water. Water tupelo was most affected by high temperature flooding (20 per cent survival), followed by black willow (47 per cent), bald cypress (60 per cent), and button bush (87 per cent). Other parameters, such as root production, showed significant differences due to both ambient and elevated temperature flooding. All species except water tupelo showed significantly lowered root production due to ambient temperature flooding, while shoot production was significantly reduced in only black willow (Table 36.1).

Within the flooded treatments, 35°C water temperatures had no effect on root or shoot biomass of any species, but 40°C decreased both shoot and root biomass of water tupelo and bald cypress. Although no statistical differences were observed between ambient and high temperature flood treatments for black willow and button bush, maximum biomass occurred in the ambient +5 (35°C) temperature treatment and minimum biomass in the ambient +10 (40°C) temperature. These two treatments did produce significant differences in shoot biomass of black willow and shoot and root biomass of button bush. This was especially obvious for button bush and may represent a distinctly different temperature optimum for this species.

Lack of morphological avoidance characteristics at elevated temperatures was assumed to indicate an environmental constraint on the acclimation process. Each of the species did produce some, but not all, of the previously listed morphological adaptations. Water tupelo produced hypertrophied stems and more lenticels in the ambient flooded treatment, but in high-temperature flooded environments neither of these adaptations was pronounced. Bald cypress stems were less hypertrophied in the 40°C flooded environment than in the ambient flooded environments, but they produced few adventitious roots and lenticels compared to none in the ambient flooded environment. In the 40°C flooded treatment, black willow produced 15 times less adventitious root biomass and

Table 36.1: Mean shoot and root biomass (gdw) of seedlings of four woody species grown in drained (DR) and flooded (FL) water level treatments at ambient (LW), mid- (MD) and high- (HG) temperature regimes. Different letters for a parameter indicate statistical differences at alpha level = 0.05

			Biomass	
			Shoot	Root
<u>Nyssa aquatica</u>	LWDR	12.0 AB ^a		25.7 A
	LWFL	13.7 A		20.0 ABC
	MDFL	14.3 A		17.6 BC
	HGFL	2.8 C		3.0 E
<u>Taxodium distichum</u>	LWDR	13.1 A		32.7 A
	LWFL	11.7 A		17.3 BC
	MDFL	10.3 A		13.0 C
	HGFL	2.3 B		1.2 D
<u>Salix nigra</u>	LWDR	69.0 A		104.9 A
	LWFL	29.2 CDE		29.7 CD
	MDFL	33.3 BCD		34.6 BCD
	HGFL	3.8 E		1.9 D
<u>Cephalanthus occidentalis</u>	LWDR	17.8 ABC		30.4 AB
	LWFL	15.5 ABC		14.6 CD
	MDFL	26.9 A		18.2 BC
	HGFL	12.1 C		5.0 D

Note: a, Statistical analyses for these data includes all data from a 3 x 3 factorial experiment including the four treatments exhibited in these tables. Consequently the lettering representing the multiple range test may appear inconsistent.

fewer lenticels than at ambient temperature, but had no stem hypertrophy regardless of temperature. In contrast, button bush produced similar adventitious root biomass and lenticel development regardless of temperature. Although no stem hypertrophy was observed for button bush in response to flooding at any temperature, the number of basal stems increased in response to high temperature flooding. This would increase the area of stem tissue serving as a potential site for gas exchange with the atmosphere, hence the effect was similar to stem hypertrophy.

Morphological modifications, linked to the internal aeration system, were reduced by higher-temperature flood treatments; water tupelo was most and button bush least affected. Hence, roots of water tupelo, bald cypress, and to a lesser extent black willow, were restricted to an anoxic environment, without the

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ability to ameliorate it through development of morphological adaptations.

Photosynthesis, transpiration, stomatal conductance and xylem pressure potential of water tupelo were not significantly altered by ambient unsaturated, ambient flooded or mid-temperature flooded conditions, but all of these metabolic functions were altered by high-temperature flooded conditions (Table 36.2). These metabolic functions were not affected in button bush as a result of any treatments. Bald cypress and black willow showed intermediate responses; willow was generally more similar to water tupelo, and bald cypress was more similar to button bush. These responses indicate the different ability of the species to acclimate to the high-temperature flooded environment and its impact on leaf metabolic functions.

Ambient temperature flooding did not affect the sugar or starch concentrations of any of the study species following the first growing season (Table 36.3). Significant reductions in both sugar and starch concentrations in bald cypress resulted from high temperature flooding. Starch, but not sugar, concentrations were significantly reduced in water tupelo by high-temperature flooding. In both these species the starch pool available for growth in the spring was reduced. In button bush and black willow seedlings only sugar concentrations were lower in the high-temperature flooded treatment. The importance of sugar concentrations in

Table 36.2: Net midday photosynthetic rate ($\mu\text{M m}^{-2}\text{s}^{-1}$), transpiration rate ($\text{mM m}^{-2}\text{s}^{-1}$), stomatal conductance ($\text{mol m}^{-2}\text{s}^{-1}$) and xylem pressure potential (-MPa) of seedlings of two woody species grown in drained (DR) and flooded (FL) water level treatments at ambient-(LW), mid- (MD), and high- (HG) temperature regimes. Different letters for a parameter indicate statistical differences at alpha level = 0.05

		Photo	Trans	Conduct	XPP
<u><i>Nyssa aquatica</i></u>	LWDR	13.0 A ^a	7.7 A	0.34 A	0.88 B
	LWFL	12.6 A	7.6 A	0.36 A	0.84 B
	MDFL	12.9 A	7.2 A	0.33 A	1.15 AB
	HGFL	-0.7 C	2.3 C	0.07 C	1.72 A
<u><i>Cephalanthus occidentalis</i></u>	LWDR	9.6 A	3.8 A	0.16 A	0.49 A
	LWFL	11.8 A	5.6 A	0.33 A	0.66 A
	MDFL	10.3 A	5.3 A	0.38 A	0.60 A
	HGFL	9.9 A	5.6 A	0.29 A	0.62 A

Note: a, Statistical analyses for these data includes all data from a 3 x 3 factorial experiment including the four treatments exhibited in these tables. Consequently, the lettering representing the multiple range test may appear inconsistent.

Table 36.3: Carbohydrate concentrations (mg gdw^{-1}) in January for seedling roots of four woody species grown in drained (DR) and flooded (FL) water level treatments at ambient- (LW), mid- (MD), and high- (HG) temperature regimes. Different letters for a parameter indicate statistical differences at alpha level = 0.05

		Sugar	Starch
<u><i>Nyssa aquatica</i></u>	LWDR	9.0 A ^a	20.3 AB
	LWFL	8.0 A	22.4 A
	MDFL	8.3 A	19.2 ABC
	HGFL	7.6 A	15.8 C
<u><i>Taxodium distichum</i></u>	LWDR	6.0 A	18.6 AB
	LWFL	5.2 A	22.2 A
	MDFL	4.7 A	14.7 BCD
	HGFL	1.9 B	6.2 E
<u><i>Salix nigra</i></u>	LWDR	8.0 A	7.5 A
	LWFL	7.3 AB	8.2 A
	MDFL	5.8 BC	7.9 A
	HGFL	1.9 D	5.9 A
<u><i>Cephalanthus occidentalis</i></u>	LWDR	13.7 A	16.5 AB
	LWFL	12.9 AB	18.5 A
	MDFL	11.9 ABC	16.4 AB
	HGFL	10.4 C	14.8 AB

Note: a, Statistical analyses for these data includes all data from a 3 x 3 factorial experiment including the four treatments exhibited in these tables. Consequently, the lettering representing the multiple range test may appear inconsistent.

dormant seedling roots is unknown, but the sugar pool does support maintenance respiration. High-temperature flooding during the winter months would cause an elevated metabolic rate and probably deplete carbohydrate reserves available for morphological acclimation or growth.

The four study species acclimated and survived continuous flooding at 30° and 35°C water temperatures, but 40°C flood water reduced morphological acclimation to varying degrees. Lack of acclimation probably shifted root metabolism toward anaerobic pathways, which subsequently affected leaf metabolic functions. What limited morphological acclimation?

As temperature increases, respiration also increases. Respiration rates of excised root tissue of water tupelo approximately doubled when incubated at 40°C compared with rates at 25°C, regardless of whether the seedlings had been grown in either 30°

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or 40°C soil temperatures (Table 36.4). Increased respiration is not usually matched proportionately by a photosynthetic increase. Consequently, the ratio of photosynthesis to respiration decreases, effectively resulting in plant starvation. At temperatures of 35°C and lower, plants can morphologically acclimate to avoid the stress as well as possible. Responses to flooding include increased ethylene production (Crawford, 1982; Reid and Bradford, 1984). Our work suggests that bald cypress and water tupelo may differ in ethylene production response, especially to shallow flooding. Thus, some species differences may exist in the threshold for and production of ethylene. Yu, Adams and Yang (1980) showed that enzymatic conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene is temperature sensitive and is greatly diminished at 35–40°C. Water tupelo and bald cypress subjected to high-temperature flooding (40°C) had 20 (0.03 vs. 0.61) and 7 times (0.4 vs. 0.29 ppm $\text{gdw}^{-1} \text{ h}^{-1}$) less ethylene production, respectively, than those in 30°C flood water. Ethylene has been correlated with stem hypertrophy and adventitious root development, and cited as largely responsible for increased cellulase activity leading to increased root aerenchyma (Drew, Jackson and Gifford, 1979). Inhibition of ethylene formation by high temperature may be responsible for the lack of morphological acclimation. When water tupelo seedlings were exposed to alternating two-week intervals of ambient (~30°C) saturated soil and 38°C flooded conditions, stem hypertrophy occurred only above the flood water. In the zone exposed to 38°C flood water above the soil surface, no stem hypertrophy was observed. The exact temperature causing the inhibition of ethylene formation is probably different among species, with that for button bush higher than that for water tupelo. Above this critical temperature, the plant's ability to acclimate morphologically is reduced. The plant may depend proportionately more on anaerobic metabolism, accelerated by high temperature, with all its inherent inefficiencies and toxic end-

Table 36.4: Mean excised root respiration ($\mu\text{M CO}_2 \text{ gdw}^{-1} \text{ s}^{-1}$) at two incubation temperatures for *Nyssa aquatica* (water tupelo) grown in unsaturated, shallowly flooded, and deeply flooded water regimes at ambient (30°C) and high (40°C) water temperatures.

	Incubation temperature (°C)	Growth temperature 30°C	Growth temperature 40°C
Unsaturated	25	0.011	0.012
	40	0.039	0.030
Shallowly flooded	25	0.013	0.011
	40	0.041	0.029
Deeply flooded	25	0.014	0.006
	40	0.038	0.011

products. The end result is probably earlier death, due to the combined effects of the high temperature/flooding stress.

The temperature of primary injury at which root membrane integrity is lost is also important. Differences among these four species using the electrolyte leakage method (Ingram and Buchanan, 1984) have been observed, with button bush and water tupelo being similar and having greater temperature stability than black willow and bald cypress. Thus membrane temperature stability might restrict some species, while others are restricted by other plant responses.

Increasing flood water temperature may affect soil aeration similarly to simply increasing the flood water depth. Gur *et al.* (1972) reported that increasing the temperature of an unsaturated soil promoted anoxic conditions in the root due to accelerated metabolism. Decreased O₂ solubility in higher temperature water, in conjunction with accelerated metabolism, would further lower the O₂ content of the substrate. Thus, a temperature increase would decrease the oxygen supply to the substrate, as does increasing the diffusion path length by increasing the flood water depth. This compound effect is even more important when the plant cannot acclimate, since diffusion through the water column and into the substrate is the only method of transporting O₂ to the plant roots.

Why and how do species differ in their thermal tolerance? A primarily southern geographical distribution or tropical or subtropical origin of a plant family has generally been thought to result in greater thermal tolerance. Geographic ranges of water tupelo, black willow, bald cypress and button bush include the southeastern coastal plain, although only the latter two species reach the southern tip of Florida. However, these species belong to plant families of temperate origin, except button bush of the Rubiaceae. Rubiaceae are distributed primarily in tropical and subtropical areas (Cronquist, 1981). These distributions and origins conform to the relative thermal tolerances observed for these species. A mechanism has been observed in cattails that might help explain different species temperature sensitivities. There are six major malate dehydrogenase isoenzymes in cattail. Three of these isoenzymes, with higher temperature tolerance, were found in a species that dominates the warmer portion of a thermally affected reservoir (Liu, Sharitz and Smith, 1978). A second cattail species found primarily in the cooler portions of the reservoir had isoenzymes with lesser thermal tolerance. Thus, the enzyme activity of the isoenzymes of the two species may dictate thermal tolerance.

SUMMARY

Seedlings of four tree species differed in their responses to elevated temperature flood events, depending on their ability to acclimate morphologically. Button bush plants, which best acclimated to elevated temperature flood conditions, grew and responded physiologically similarly to those grown in ambient temperature flood conditions. The three species that did not acclimate to the elevated temperature flood had lower survival, less biomass and altered physiological responses. Several results from

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the literature can help explain the lack of acclimation. First, morphological acclimation, producing an internal aeration system (aerenchyma, stem hypertrophy and adventitious root formation), has been correlated with ethylene production. Second, ethylene is regulated by a temperature-sensitive enzymatic conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene. Hence, the key to survival in elevated temperature flood waters is the ability to acclimate to that environment.

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Chapter Thirty-seven

ULTRASTRUCTURE STUDIES AS A MEANS OF EVALUATING PLANT TOLERANCE TO FLOODING

B.B. Vartapetian

INTRODUCTION

During the last 15 years electron-microscopy has been widely used in a number of laboratories for the investigation of plant cell injury and plant adaptations to hypoxia and anoxia. The advantage of this approach is that it makes possible the visualization of plant cell fine structure under the extreme conditions provoked by the experiment or by nature. The study of cell fine structure under the extreme conditions of oxygen deficiency is of special importance because it has been used in a number of cases to solve the physiological or ecological problems connected with plant flooding adaptations. For this reason the electron-microscopic technique has been used extensively in the author's laboratory for studying plant life under flooding conditions.

This chapter demonstrates how the methods of experimental cytology can be used by plant physiologists or ecologists as a tool for solving theoretical and applied problems connected with the phenomena of hypoxia and anoxia brought about by flooding conditions.

The value of structural studies for solving functional questions connected with plant flooding became apparent under hypoxia and anoxia conditions when it was found that a number of typical changes in plant cell ultrastructure took place. Mitochondrial ultrastructure changes were most obvious and were thought to be of diagnostic significance. Being the organelles of oxygen metabolism, mitochondria should naturally suffer first of all and most of all when the plant cell is restricted of oxygen.

After many years of plant cell ultrastructure observations under different oxygen stress conditions, it became evident that mitochondrial membrane rearrangements under oxygen stress occur in a definite sequence. In some cases, as already mentioned, these rearrangements may be of importance for diagnoses of cell oxygen supply. In other cases they permit the evaluation of the reversibility or irreversibility of the changes taking place in the cell under oxygen stress. Thus, by observing the peculiarities of mitochondrial membrane rearrangements under flooding, one can judge the adaptive capabilities of plant cells under extreme conditions. A few examples taken from the experiments carried out in the author's laboratory in the Institute of Plant Physiology Acad-

emy of Sciences of USSR, Moscow will be used to illustrate this technique.

EXAMPLE 1: Supersensitivity of Flood-Tolerant Plant Root Ultrastructure to Oxygen Deficiency

The ultrastructure of a detached pumpkin root cell is shown in Figure 37.1(a) under normal aerobic conditions at 20°C. After 12 h of anoxia (Figure 37.1b), pathological changes in mitochondrial structure are evident: marked swelling, reduction of cristae number, and the matrix becomes transparent. Complete destruction of both the mitochondria and other organelles occurs after 24 h (Figure 37.1c). If the temperature was elevated from 20°C to 32°C the time of the destructive changes in mitochondria under anoxia was cut in half (Vartapetian, Andreeva and Maslova, 1972a). At 42°C, irreversible degradation of mitochondrial membrane took place after only 15–30 minutes of anoxia.

Anaerobic conditions arising in the root zone with flooding and subsequent irreversible destruction of cell ultrastructure is often a reason for the whole plant death. In a number of cases it is associated with mass losses of agricultural plants.

However, a great number of wild, higher plant species are not injured by anaerobic soils. Moreover, they normally grow in the waterlogged soils that are unsuitable for other species and especially for cultivated plants. An exception of this ecological group among the agricultural plants is rice, which is usually cultivated on periodically flooded soils.

A number of theories have been proposed to explain why some plant species are more tolerant to root hypoxia or anoxia than others.

One popular theory is that the plant's survival is related to metabolic adaptations of the roots, i.e. the adaptation is of a biochemical nature (Crawford and McManmon, 1968; McManmon and Crawford, 1971; Crawford, 1978, 1980; Chirkova, Khazova and Astafurova, 1974; Chirkova, 1975).

Contrary to the biochemical theory mentioned, another alternative was advanced based on the results of electron-microscopic investigations of roots under anoxia (Vartapetian, Andreeva, Maslova and Davtian, 1970). A paradoxical phenomenon was demonstrated: ultrastructure of root cells of flood-tolerant plants appeared to be very sensitive to oxygen deficiency. The paradox was that the root ultrastructure of hydrophytes – rice, sedge – put under anoxic conditions were more sensitive to injury than roots of mesophytes (Figure 37.2) (Vartapetian et al., 1970; Vartapetian, 1982).

Recently, similar results were obtained with three other hydrophytes – Alisma plantago aquatica L., Lycopus europeaus L. and Glyceria aquatica L. – (Vartapetian and Andreeva, 1986). This made it possible to question the basis of biochemical theory of plant adaptation to flooded soils as a viable concept. According to the results of Vartapetian et al., (1970) and Vartapetian (1978), the adaptations of these plants occur not at the biochemical (molecular) level (i.e. due to the peculiarities of their metabolism),

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Figure 37.1: Ultrastructure of detached pumpkin (Cucurbita pepo L.) root cells: (a) aerobic conditions (control); (b) anoxia 12 hours; (c) the same 24 hours. M, mitochondria; L, lipid droplet.

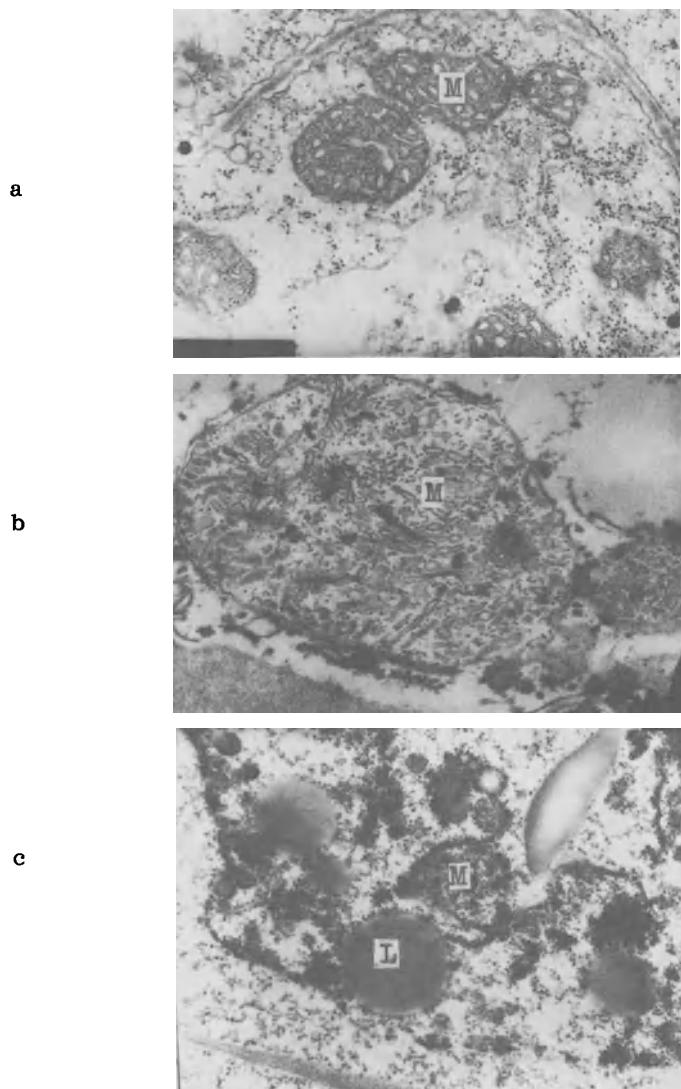
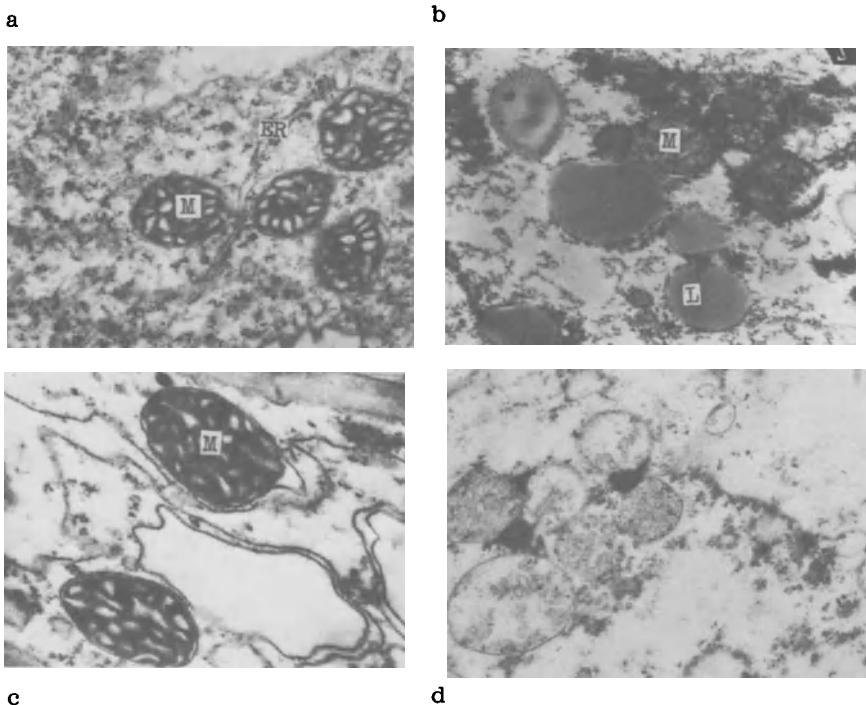


Figure 37.2: Ultrastructure of detached rice (*Oryza sativa* L.) and sedge (*Carex leporina* L.) roots under aerobic and anaerobic conditions: (a) rice, aerobic conditions (control); (b) rice, anoxic conditions 12 hours; (c) sedge, aerobic conditions (control); (d) sedge, anoxia 12 hours. ER, endoplasmic reticulum.



but mainly on the level of the whole plant. Due to oxygen transport from overground aerated parts to the roots, facilitated by the presence of aerenchyma in the plants of this ecological type, the root cells appear to avoid anaerobiosis rather than adapt to it. Hence, the tolerance is more apparent than true resistance of plant root cells to anoxia (Vartapetian, 1978).

The conclusions based on ultrastructural studies were later confirmed by Webb and Armstrong (1983) in the experiments with the hydrophyte rice and two mesophytes, pumpkin and pea. They demonstrated that among these plants the most sensitive to oxygen deficiency was the roots of rice, not the roots of pumpkin or pea. Webb and Armstrong came to the conclusion that the idea of high resistance to anoxia of root cells of rice and other plants growing on anaerobic soils was questionable.

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ApRees and Wilson (1984), using [^{14}C]-saccarose for studying protein synthesis in the roots of flood-tolerant Glyceria and non-tolerant Pisum under anoxia and hypoxia, concluded the same. They could not show any advantage of flood-tolerant Glyceria as compared to non-tolerant Pisum. Moreover, they found that in relation to protein synthesis Glyceria roots were more sensitive to O₂ deficiency than those of Pisum.

Hence, ultrastructure investigations have played an important role in uncovering one of the main strategies of higher plant adaptation to flooded soils.

EXAMPLE 2: End-Products of Anaerobic Metabolism and Plant Injury

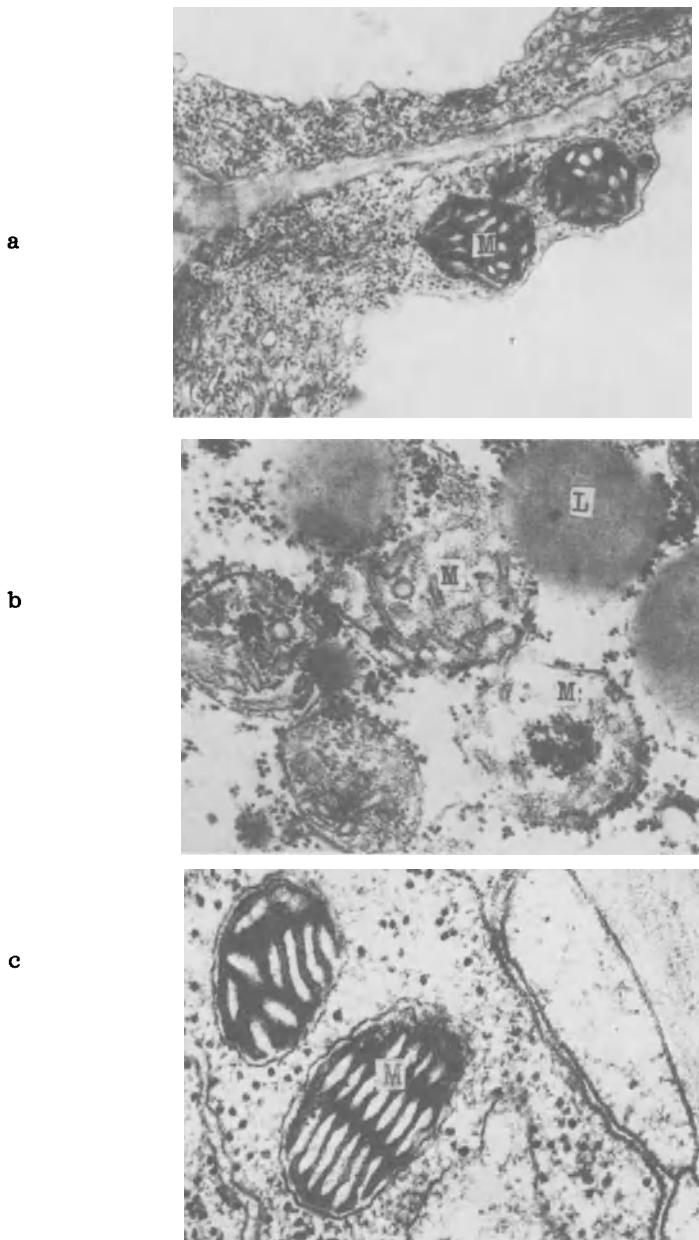
The ultrastructural investigations of plant cells also helped to understand the role of end-products of anaerobic metabolism as a cause of plant injury in the absence of oxygen. Many specialists in plant anaerobiosis suggested that the end-products of anaerobic carbohydrate metabolism, mainly ethanol, were the main factors in plant injury in an oxygen-free medium because they accumulate in plant cells under anoxia and some are toxic to cells. It was suggested that inhibition or weakening of glycolitic end-product formation (ethanol) is the mechanism of the flood-tolerant plants' adaptation to anaerobic environment (McManmon and Crawford, 1971; Crawford, 1978; Chirkova *et al.*, 1974; Chirkova and Semenov, 1979).

However, special investigations of this question carried out also with the help of electron-microscopy led to the opposite conclusion (Vartapetian, Andreeva and Kozlova, 1976; Vartapetian, Andreeva, Kozlova and Agapova, 1977). In particular, it was demonstrated that intensification of glycolysis under anaerobic conditions by means of plant cell feeding with exogenous glucose (i.e. intensification and maintenance of ethanol and other anaerobic products formation) did not lead to plant cell injury, and, on the contrary, it even prevented cell membrane destruction at strict anoxia (Figures 37.3 and 37.4).

Normally when detached rice or pumpkin roots (or coleoptiles or leaves) were put under anaerobic conditions, after 10-20 h one could observe that destruction of both mitochondrial and other organelles membranes took place (Figures 37.1 and 37.2). However, cell membrane degradation could be easily prevented, if under the same conditions of anoxia, plant cells were fed with exogenous glucose (i.e. artificially supplying the substrate), which supported or stimulated the fermentation, and, consequently, the formation of its end-products. However, feeding under anoxia did not prevent the ultrastructure degradation in roots of some hydrophytes which were supersensitive to oxygen deficiency (Vartapetian, 1982.). Under such conditions, fine structure of mitochondria and other cell organelles remained intact for 2-3 days and even for 5 days, instead of 10-20 h. (Figures 37.3 and 37.4).

Based on these results, the conclusion was that 'under anoxia, degradation of the organelles obviously was not the result of poisoning by toxic products of anaerobic metabolism' (Vartapetian

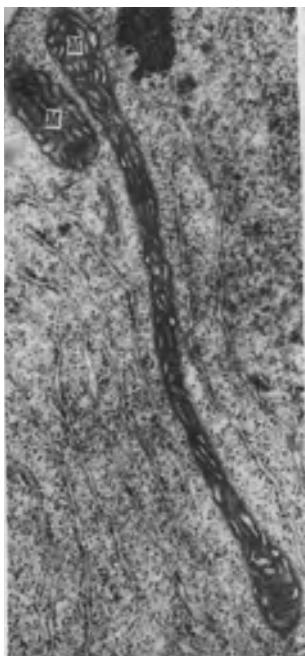
Figure 37.3: Ultrastructure of detached rice (*Oryza sativa* L.) leaves under anoxia and exogenous glucose feeding:
(a) aerobic conditions (control), without glucose feeding;
(b) anoxia 48 hours with glucose feeding;
(c) anoxia 72 hours with glucose feeding.



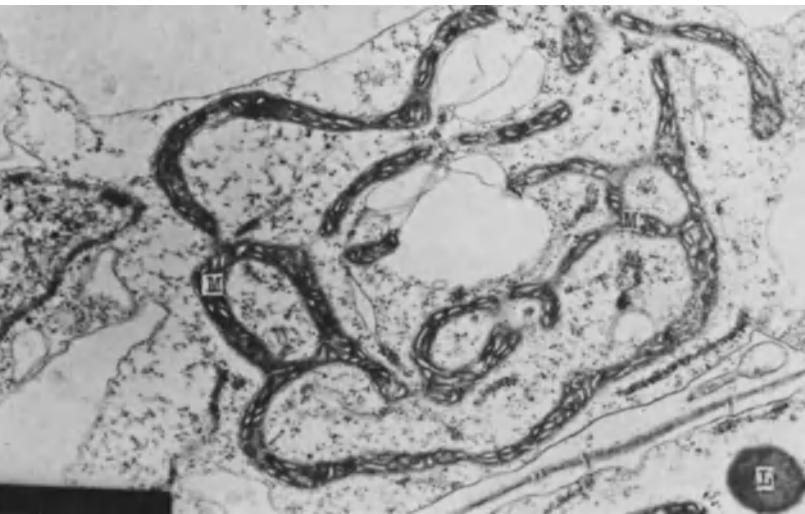
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Figure 37.4: Ultrastructure of detached pumpkin roots under anoxia and glucose feeding: (a) 24 h; (b) 72 h; (c) 120 h.

a



b



c

et al., 1976). Webb and Armstrong (1983), also demonstrated in the experiments with rice, pumpkin and pea roots the possibility of prolonging the viability of roots under anoxia by feeding with exogenous sugar.

Hence, via the use of ultrastructural investigations, it was proved that the role of ethanol and other products of anaerobic metabolism formed in plant tissues during flooding was not a damaging factor. On the contrary, endogenous formation of these products was stimulated by glucose feeding and appeared to prevent cell degradation for a relatively long time period.

This conclusion was supported by direct experiments on the effect of exogenous ethanol or organelles under anoxia carried out by Jackson, Herman and Goodenough, (1982) and Crawford and Vartapetian (1984). It was shown in these experiments that the concentrations of ethanol causing plant damage or degradation of cell ultrastructure under the anaerobic conditions were much higher than the concentrations usually detected in plant tissue under anaerobiosis.

Similarly, Roberts, Callis, Jardetzky and Walbot (1984), using nuclear-magnetic-resonance techniques, demonstrated that mutant maize plants, devoid of the key glycolytic enzyme-alcohol dehydrogenase (ADH-I-and, hence, unable to produce ethanol), were injured under hypoxia in a shorter time period than control plants containing ADH-I.

EXAMPLE 3: Super Resistance of Plant Cell Ultrastructure to Anoxia

The question arises: Is the translocation of O_2 from aerated parts of plants to roots in an anaerobic environment the unique strategy of higher plant adaptation to flooded soils? The answer is no. There is a second general strategy of plant adaptation to flooding, which can be labelled as a biochemical adaptation.

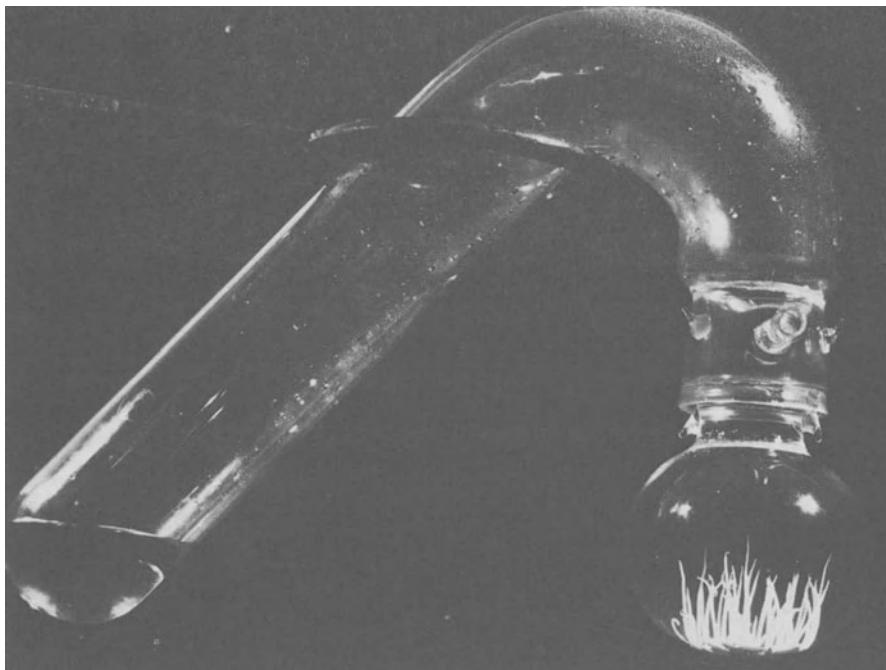
Excellent examples of plants that are biochemically and metabolically adapted to flooding are germinating rice seeds. Rice seeds germinate easily under a water layer, i.e. under hypoxia (Kordan, 1972, 1974) and it is well documented that rice seeds germinate even under strict anoxia (Vartapetian, Maslova and Andreeva, 1972b; Tsuji, 1972; Costes, Vartapetian, 1978).

Six-day-old rice seedlings germinated in a special apparatus from which all the traces of O_2 were removed by vacuum, hence, the germination took place in strict anoxia (Figure 37.5) (Costes and Vartapetian, 1978). Electron-micrographs (Figure 37.6) showed that the cells of the rice coleoptiles grown under such anoxic conditions contained all subcellular structures, including structurally intact mitochondria (Vartapetian, Andreeva and Maslova, 1971; Vartapetian et al., 1972b; Ueda and Tsuji, 1971; Tsuji, 1972, 1973; Opik, 1973). Biochemical investigations (Vartapetian, Maslova and Andreeva, 1975) demonstrated that these mitochondria contained respiratory enzymes, including cytochromes a, b, c.

Mitochondria isolated from anaerobically grown coleoptile cells were able to absorb O_2 and oxidize the substrates of the Krebs

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Figure 37.5: 6-day rice seedlings grown in a vacuum



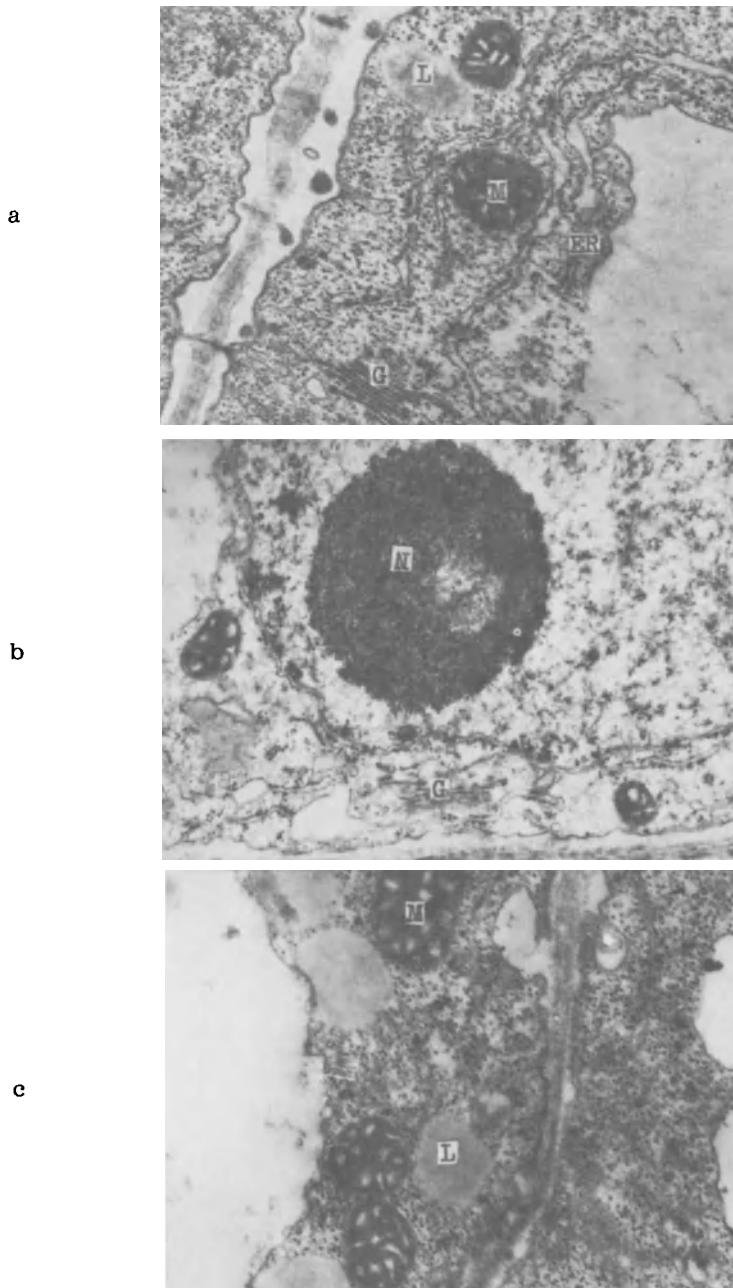
cycle (Figure 37.7). This oxidation was coupled by the phosphorylation of ADP to ATP (Costes and Vartapetian, 1978).

Kennedy, Barrett, VanderZee and Rumpho, (1980) and Kennedy, Rumpho and VanderZee, (1983) found that Echinochloa seeds were able to germinate under strict anoxia and contained functionally active mitochondria. Barclay and Crawford (1982) and Brandle (1980, 1983) demonstrated that rhizomes of some hydrophytes also served as an excellent example of this type of plant. In the case of germinating seeds of rice and Echinochloa and rhizomes, biochemical adaptation occurs, which enables the cells of some organelles to function in the complete absence of oxygen. Such plants are truly resistant to anoxia as compared to the plants with apparent resistance, which is based on the ability to transport O₂ from aerated to non-aerated parts of the plant.

Hence, the use of ultrastructural investigations has played an important role in verifying the two main strategies of plant adaptation to flooded soils (Vartapetian, 1978).

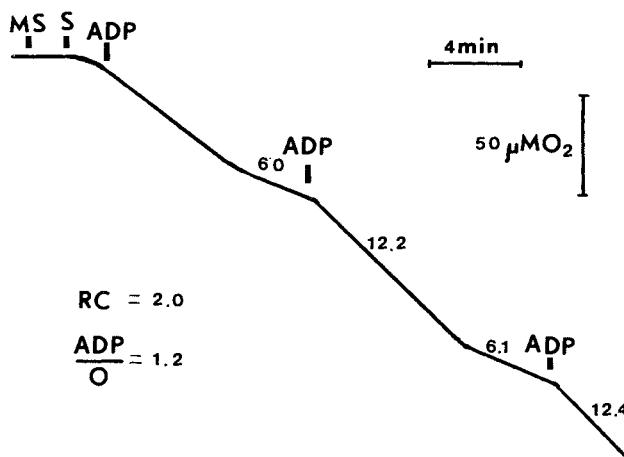
Therefore, plants have been classified in relation to their resistance to flooding into three categories: (1) truly resistant, (2) apparent resistant, and (3) non-resistant (Vartapetian, 1978). Most mesophytes are classified as 'non-resistant' plants. Unfortunately, most of the cultivated plants belong to this category,

Figure 37.6: Ultrastructure of the rice coleoptile grown in air (a) and in a vacuum (b,c). N, nucleus; G, dictyosomes.



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Figure 37.7: O_2 absorption by mitochondria from rice coleoptiles, grown in a vacuum. Introduction into a polarographic cell of: MS, mitochondrial suspension; S, succinate; ADP, adenosine diphosphate; RC, respiratory control.



causing a real problem when farmers attempt to cultivate them on wet sites.

Of course, not all species fit nicely into these three categories. With a great number of plant species and diverse environmental conditions, species seldom exhibit these attributes clearly. Moreover, the same species may have different mechanisms of adaptation depending on the stage of ontogenesis. For instance, germinating rice and *Echinochloa* seeds are truly resistant to anoxia, whereas the same mature plants have apparent resistance to anoxia. The primary roots of a non-resistant mesophyte, such as maize or sunflower, die under flooding and are replaced by adventitious roots with aerenchyma facilitating O_2 transport. The mechanism of intracellular spaces formation in these cases and the role of ethylene in the phenomenon has been documented in detail in very elegant experiments (Drew, Jackson and Giffard, 1979; Drew, Jackson, Giffard and Campbell, 1981; Jackson, 1982, 1985).

EXAMPLE 4: Long-Term Stabilization of Mitochondrial Membrane Under Strict Anoxia

The last example will demonstrate how the ultrastructural and functional studies of plant mitochondria under anoxia and post-anoxia can be used to make valuable contributions to the under-

standing of functional and structural relations of mitochondrial membrane.

First, it is necessary to make a short excursion into molecular biology of facultative anaerobic yeast mitochondria. The latter were extensively used during the last decades for studying the biogenesis of mitochondrial membranes and for determining the roles of nucleus and mitochondrial genetic systems the biogenesis of mitochondria (Schatz, 1970; Linnane, Haslam, Lukins and Nagley, 1972; Luzikov 1985).

The facultative yeasts are very convenient objects for these purposes, for when they are transferred from growing in the presence of oxygen to anoxia, mitochondrial degradation occurs rapidly (after 2-3 h). The mitochondria are transformed into promitochondria, i.e. organella without cristae. Simultaneously with the degradation of mitochondrial structure, the respiratory function of yeast is also fully lost, i.e. the yeasts are unable to absorb O₂ from the medium. Only after transferring such yeasts from anaerobic into aerobic conditions can normally functioning mitochondria be restored.

Luzikov, Zubatov and Rainina (1973) demonstrated that structural and functional degradation of mitochondria occurred not only in anaerobic medium but even when yeasts were preserved under the normal aerobic conditions and electron transport in the mitochondrial respiratory chain was inhibited by cyanide.

All these observations provided substance for the following biological generalization: the intactness of mitochondrial membranes (i.e. their ultrastructure and function) can be stabilized and maintained only under the conditions of continuous electron transport in the mitochondrial respiratory chain. As soon as electron transport and coupled phosphorylation of ADP to ATP stops, mitochondrial membrane destabilization and structural and functional degradation occur. Hence, according to this generalization, the stabilization of mitochondrial membranes can be maintained only by ATP of intramitochondrial origin.

After this short excursion into molecular biology of yeast mitochondria let us return to the results of the experiments with higher plant mitochondria under flooding or strict anoxia.

From the experimental material presented above (electron-microscopic and biochemical), it is apparent with rice and pumpkin, that the situation with higher plant mitochondria is quite different. Even long-term blocking of the electron transport in mitochondrial membranes of plants investigated by anoxia (when oxidative phosphorylation in mitochondria was fully stopped) did not result in the destabilization and destruction of mitochondrial membrane fine organization, when the plant cells were supplied with the substrate for fermentation.

Hence, based on these results, one can conclude that the structural and functional organization of plant mitochondria mentioned can be maintained and stabilized if a plant cell is abundantly supplied with ATP of extramitochondrial (glycolytic) origin.

This conclusion was strongly supported in the experiments with apple fruits (containing large reserves of endogenous sugars): mitochondrial ultrastructure of apple fruits could be

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preserved under strict anoxia for 2-3 weeks (Vartapetian, Generozova, Andreev and Vartapetian 1985).

Moreover, recent experiments with maize seeds imbibed under strict anaerobic conditions (primary anoxia), demonstrated that not only long-term stabilization of mitochondrial membrane, but even self-assembly of structurally intact and functionally active mitochondrial membrane occurred in the seed embryo at the expense of glycolitic origin ATP (Vartapetian et al., 1983, 1986). Destructive phenomena in the ultrastructure of mitochondria observed in short-term anoxia are probably the result of ultrastructure reconstruction of these organelles as a consequence of glycolytic stimulation.

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Chapter Thirty-eight

USE OF OXYGEN MICROELECTRODES TO MEASURE AERATION IN THE ROOTS OF INTACT TREE SEEDLINGS

Donal D. Hook and Martha R. McKeelin

Oxygen microelectrodes have not been widely used in studying root aeration in plants despite their potential for providing unique information on internal aeration of intact roots. Fiscus and Kramer (1970) and Vartapetian (1973) were among the first to place a small platinum electrode inside an intact root segment to measure internal oxygen partial pressure. Fiscus and Kramer (1970) used a 254 μm diameter platinum wire to measure radial movement of oxygen in excised roots of corn and jackbean. Vartapetian (1973) used a small electrode (diameter not specified) inside and outside of the roots on 50-day-old pumpkin plants to show that oxygen did not readily diffuse from the atmosphere to the roots of these plants via the stem. Bowling (1973) was probably the first to use a true microelectrode in measuring oxygen partial pressure in intact sections of plant roots. He mounted excised roots of sunflower (about 1 cm long and 400-500 μm diameter) between two cover slips and viewed at 640 \times magnification. A 1 μm diameter oxygen microelectrode was pushed through the cells by a micromanipulator to measure oxygen partial pressure at specific locations in the root.

Tjepkema and Yocom (1974) and Tjepkema (1983) used an oxygen microelectrode to measure oxygen partial pressure in the nitrogen-fixing nodules of soybeans (*Glycine max*. Merr.) and *Myrica gale* L. To our knowledge, no one has used a microelectrode to evaluate oxygen movement from atmosphere to root via the stem in wetland plants. Armstrong (1979) used a cylindrical platinum electrode placed around roots to measure rate of oxygen loss (ROL) from plant roots and a series of equations (Armstrong, Healy and Lythe, 1983) to estimate internal aeration of the roots. Armstrong's techniques have proven successful for measuring ROL but require several assumptions concerning pore-space resistance and respiration demand for estimating internal aeration. Even with reasonable estimates of these factors (which are hard to obtain for each species and change with growth condition), his methods only give an estimate of overall internal oxygen concentration; they do not provide a means of evaluating compartmentalization of aeration.

Several problems must be overcome in order effectively to utilize the oxygen microelectrode in studying root aeration: (1) tissue must be soft enough for the electrode to penetrate without breaking; (2) tissue must be held firmly in place; (3) electrode penetration must be done with a micromanipulator equipped with a

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micrometer to reduce electrode breakage and to determine depth of penetration; (4) roots must be shielded from atmospheric oxygen during measurement, if internal aeration is to be studied; (5) sections of roots must be observed under magnification (6 to 50 x or more) to determine approximate loci at each reading site, and (6) provisions must be made for calibrating the electrode inside the tissue.

Of these problems, calibration of the microelectrode in the tissue is the most difficult to overcome. Tjepkema and Yocom (1974) and Tjepkema (1983) pointed out that the relationship between external calibration of the electrode in air-equilibrated agar (containing 0.1 M KC1) and the readings in the tissue were only approximate. Distortions due to dissolved substances and uneven distribution of intercellular air spaces in tissue and their effect on the electrode could not be accurately calculated by their method. Thus, Tjepkema and Yocom (1974) stated that the electrode readings can only be qualitatively related to oxygen concentration in the plant tissue.

A method is presented here that permits the measurement of relative oxygen partial pressure in the media surrounding the roots, the rhizosphere and at various depths within the root. By obtaining free hand or mounted root sections, and observing under the microscope in conjunction with micrometer readings, the approximate position of the electrode in the tissue at each reading may be verified. Also, means of verifying whether the electrode was measuring static oxygen partial pressures or gas exchange from the atmosphere through the stem to the root are presented.

METHODS

Equipment*

A micro-volt-ampmeter (Chemical Microsensor Model 1201), calibration cell, oxygen microelectrode (Model 723 with 2-3 mm diameter tip with recessed gold cathode covered by a special oxygen-permeable membrane), silver-silver chloride electrode (Model 334), and two miniature electrode holders (Model 1108) were obtained from Transidyne General Corporation. (These products are now sold by Diamond Electro-Tech, Inc.) Other equipment used were a strip chart recorder; micromanipulator (Brinkman Model MM33); fiber optic illuminator with twin lights; and binocular dissecting microscope with 6 to 50 x magnification, with a mechanical stage capable of a large range of X-Y movement and large mount-holding device (we used a A/O Spencer Model 1825 Attachable Mechanical Stage and mounted it on the base of a Wild Binocular Microscope on a 0.25 in thick plexiglass plate).

A plexiglass V-shaped trough was constructed of 6mm in thick plexiglass with a small V in the bottom to hold the agar plug

* Mention of trade names are for identification purposes and does not imply or mean that Clemson University recommends this product.

(containing the roots) rigidly in position. This apparatus was cut to fit into the mechanical stage holder. Four tanks of gas (0, 2, 10 and 21 per cent oxygen) were used to calibrate the micro-electrode and a Lab-Crest pressure tube flowmeter was used to measure gas flow rate.

Plant Material and Agar

Seedlings of loblolly pine (*Pinus taeda* L.), swamp tupelo (*Nyssa sylvatica* var. *biflora* Walt. Sarg.,), and water tupelo (*Nyssa aquatica* L.) were germinated and grown in (a) well-drained or flooded pots in a glasshouse or growth chamber and (b) in flooded or alternately flooded/drained soils in soil tanks (Hook and Stubbs, 1967). The soil was a Betheira series and length of flooding treatments varied from one month to one year. At harvest, seedlings were gently washed from the soil with a hose using tap water and stored with roots in deoxygenated water until they were placed in agar.

A 1.5-2.0 per cent (w/v) solution of agar was made by placing agar in boiling 0.1 M KC1 solution and cooled with nitrogen gas bubbling through the solution until the agar temperature was about 42°C. Seedling roots were placed in large test tubes (24 mm x 15 cm) or plastic pipes (4.1 cm x 21 cm) with one end sealed with a rubber stopper and the cooled agar (42-45°C) was poured into the container until it covered the roots up to the root collar.

After the agar had solidified, the intact seedling with the agar plug around the roots was gently removed from the container and placed horizontally on the V-trough plastic holder on the mechanical stage. A small plastic bag was placed over the top of the seedling and loosely attached around the top of the agar plug. The plug of agar was manually rotated until a suitable root tip was visible near the surface of the agar. The visible root tip was manipulated into the microscope's field of vision with the mechanical stage. Fiber optics light permitted high illumination for long periods with very little drying or heating of the agar.

Calibration Procedure

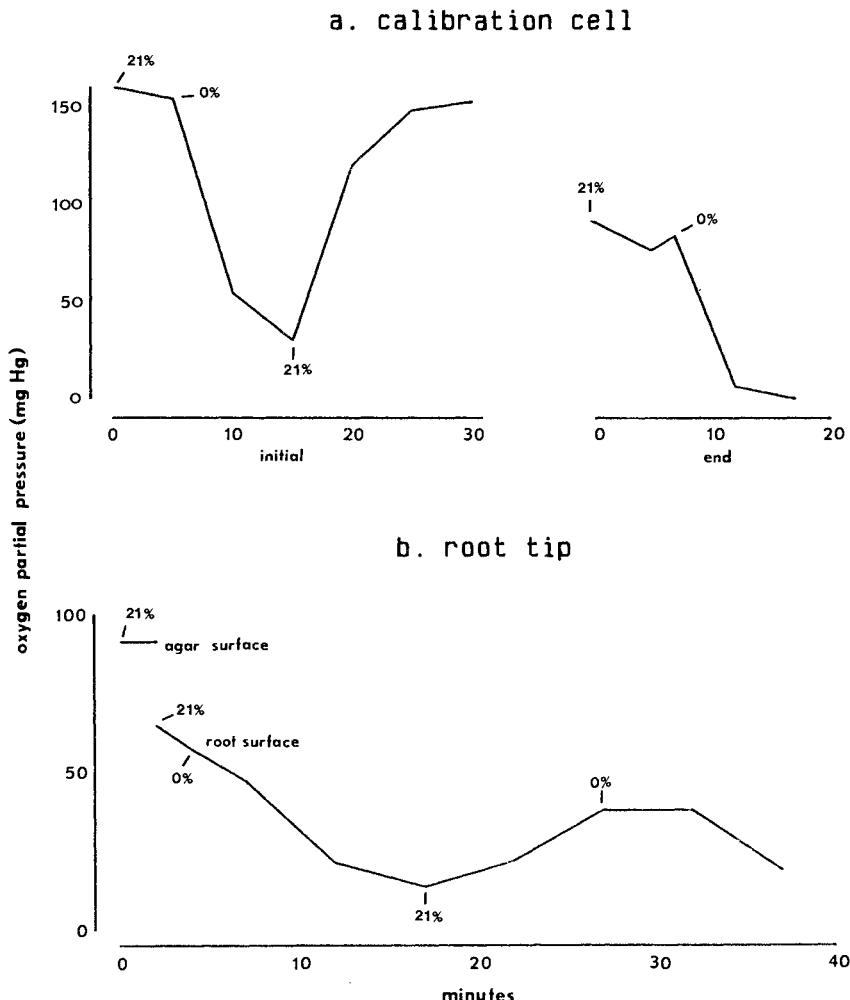
Prior to use, each oxygen microelectrode was placed in a calibration cell and current flow was read between the microelectrode and reference electrode at 0.1 volt intervals from -0.1 to -1.0 volt applied to the microelectrode to develop a characteristic curve (Poel 1960). From the curve a polarization voltage of -0.750V was selected.

Response of microelectrodes to oxygen was measured by bubbling 21 per cent oxygen through a 0.9 per cent NaCl saline solution for 5-10 min and measuring current flow and then by bubbling nitrogen through the solution (5-10 min) to establish baseline current (Figure 38.1a). Also various concentrations of oxygen and nitrogen were used to develop a standard curve.

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Figure 38.1: Microelectrode calibration and response to oxygen partial pressures in agar and rhizosphere.

(a) Calibration response to 21% and 0% oxygen at beginning and end of 5 hour run. (b) Oxygen partial pressure at agar surface and response of water tupelo rhizosphere to atmosphere oxygen changes.



Measurement Procedures

The calibrated oxygen microelectrode was removed from the calibration cell and placed in the micromanipulator. With the reference electrode inserted in the agar plug and held in position with a clamp, the microelectrode was brought to touch the surface of the agar using the micromanipulator. Settings on the micromanipulator (mm scale and μm vernier) and the current flow were recorded. This gave a current flow (oxygen partial pressure) for air-saturated agar. As the microelectrode was advanced into the agar, current readings were made at various depths. Usually current flow dropped significantly with increasing depth in the agar and stabilized at a low reading. When the electrode touched the root surface the verniers and current flow were read and recorded. The microelectrode was pushed into the root at desired intervals. At each position the verniers and current flow were read.

The desired gas was passed through the plastic bag at a low flow rate over the top of the seedling. Air flow through the bag was 80 ± 20 ml/min and was insufficient flow to inflate the bag, hence, no increase in pressure was produced around the exposed seedling. However, the flow rate was sufficient to displace existing gas in the bag as was evidenced by rapid response of electrode current to various oxygen-nitrogen mixtures.

RESULTS AND DISCUSSION

The microelectrodes were easily broken but with care they could be placed in the succulent root tips of loblolly pine, swamp tupelo and water tupelo seedlings as long as vibrations were held to a minimum and the angle of approach was 40° or more. When the angle of approach became more acute than 40° there was a tendency for the electrode to slide along the root surface, bend, and break.

A concentration of 1.5-2.0 per cent agar around the roots held the roots firmly in place, shielded them from atmospheric oxygen, and provided sufficient visibility so that the microelectrode could be guided to the desired loci on the root. The upper diameter limit for the agar plug appeared to be about 25 mm. Plugs with larger diameters amplified small vibrations such as focusing the stereoscope and resulted in excessive electrode breakage. Also during long experiments (4 to 6 hours) the agar shrunk slightly due to desiccation and tended to pull away from the electrode. When this occurred it was necessary to advance the microelectrode a few micrometers to maintain its location.

The agar effectively shielded the roots from direct contact with atmospheric oxygen for several hours. Visibility was also sufficient to determine when the microelectrode contacted the root surface, if roots were no deeper than 7-10 mm in the agar. Hence, the approximate depth of the microelectrode in the root could be estimated by recording the micrometer readings on the micromanipulator at root surface and each reading within the root.

By regulating the oxygen concentration in the atmosphere (plastic cover) surrounding the foliage and stem, and observing

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changes or lack of changes in oxygen partial pressure in the root or rhizosphere, it was possible to determine whether the readings were due to oxygen trapped during preparation or to gaseous exchange through the internal aeration system of the seedling.

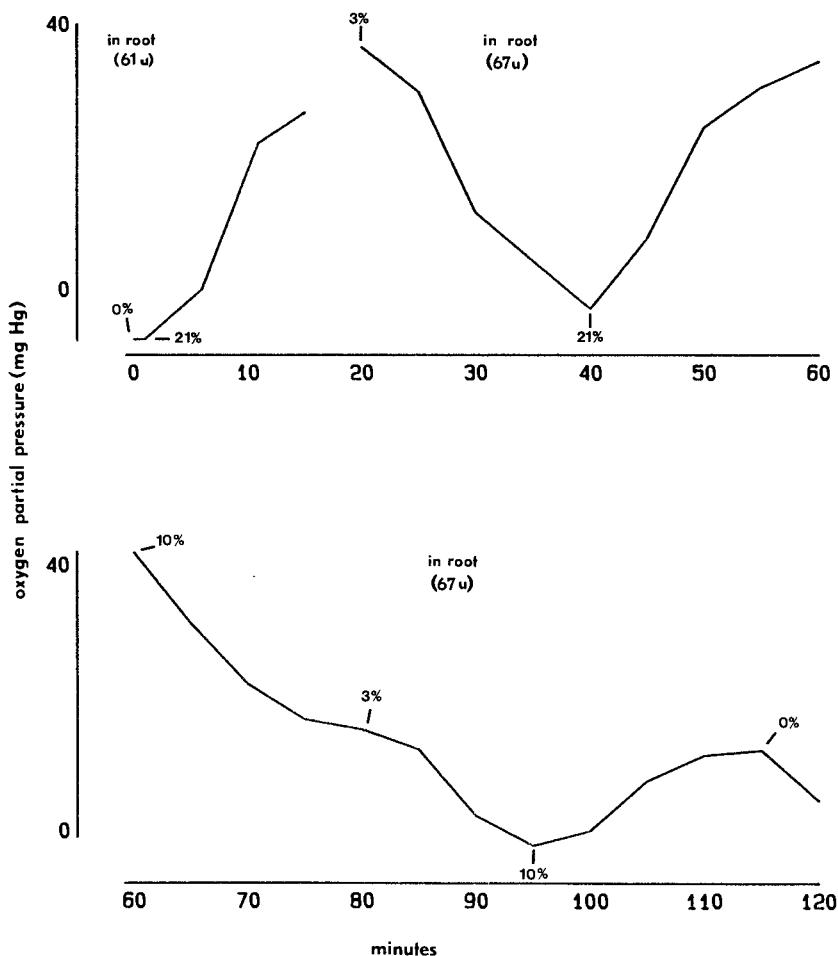
It was necessary to calibrate the electrode at the beginning and end of each experiment to (a) establish a calibration curve, (b) account for drift, and (c) determine if tissue had an effect on the electrode response (Figure 38.1a).

The oxygen partial pressure in the rhizosphere of a water tupelo root decreased to about 15.2 mm Hg (2.0×10^{-9} amps) after about 15 minutes of gassing the seedling top with 10 per cent oxygen and increased to 38.0 mm Hg (5.0×10^{-9} amps) after about 15 minutes of gassing with 21 per cent oxygen (Figure 38.1b). At a depth of about 67 μm within the root, the oxygen partial pressure was 38.0 mm Hg with 21 per cent oxygen; 13.7 mm Hg with 10 per cent oxygen and 0.0 mm Hg with 3 per cent oxygen or 0 per cent oxygen (Figure 38.2a and b).

The direct correlation between the changes in the oxygen composition of the atmosphere surrounding the top of the seedling and the oxygen partial pressure in the root or rhizosphere verified that water tupelo seedlings grown in a flooded environment had a very efficient internal aeration system. This has been previously demonstrated by dyes (Hook and Brown, 1973) and diffusion of oxygen from roots into an anaerobic solution (Keeley, 1979). The technique herein also demonstrated that 3 per cent oxygen around the foliage was not sufficient to provide a measurable oxygen partial pressure in the root (Figure 2a and b). This indicated that internal aerobic respiration consumed all available oxygen transported by the 3 per cent oxygen atmosphere before it reached the root tip. Similarly, the proportional oxygen partial pressure in the root was smaller with a 10% oxygen atmosphere around the foliage and stem than with a 21% oxygen atmosphere ($31.7 \text{ mmHg}/10\% \text{ O}_2 = 1.37$ as opposed to $41.8 \text{ mmHg}/21\% \text{ O}_2 = 1.99$). However, it seems probable that if the agar plug and intact roots were cooled to 0-to-3°C to reduce or eliminate aerobic respiration the ratios would coalesce. If this happened it would be possible to use different atmospheric concentrations of oxygen to approach an *in vivo* calibration of the microelectrode in wetland plants with well-developed aeration systems.

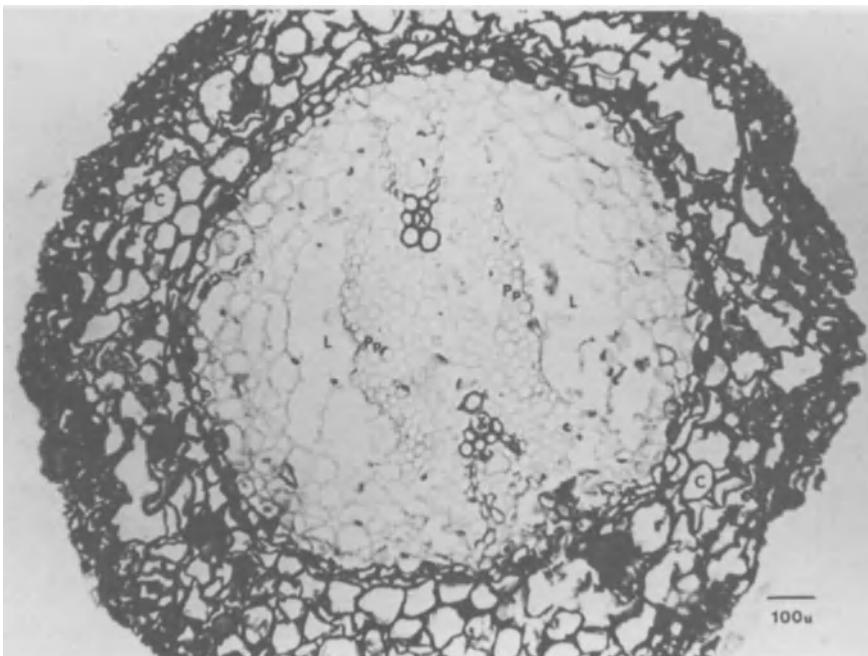
Oxygen partial pressure readings on loblolly pine seedlings (one year old or less) were usually higher inside than on the root surface and they were somewhat variable inside the root from flooded treatments (Table 38.1). Such responses indicate that very little oxygen diffused out of the actively growing loblolly pine roots. Internal aeration appeared to be compartmentalized as is shown by the variable readings at different depths inside the root. This is consistent with the development of large aerenchyma zones in loblolly pine roots under flooded conditions (Figure 38.3). More detailed descriptions of how flooding affects aerenchyma development in loblolly pine roots can be found in McKevelin (1984) and Topa (1984). Roots of loblolly pine from well-drained soils had very low oxygen partial pressures and the oxygen readings in the roots were not responsive to changes in the oxygen composition around the foliage and stem.

Figure 38.2: Oxygen partial pressures in root of water tupelo seedling at 61 and 67 μ m depths and response to atmospheric oxygen changes



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Figure 38.3: Cross-section of a flooded loblolly pine seedling root tip. Shows large aerenchyma zones (lacunae) within the stele. C, cortex; E, endodermis; Pp, protophloem; X, xylem; P, pericycle; L, lacunae



SUMMARY

The techniques presented herein overcame all obstacles to the use of the microelectrode for measuring internal or rhizosphere aeration except two. The loci of readings within the root could only be identified as to the general area or zone. Calibration in the tissue

Table 38.1: Variation in oxygen partial pressure (a) on the root surface and within the root, and (b) with oxygen-nitrogen composition around the foliage and stem of one-year-old loblolly pine seedlings

Seedling (a)	Root type	Length below root collar (cm)	Approximate depth of electrode in root (μm)			
			0	10	20	30
			PO ₂ mm Hg			
1	tap	10.5	34.2	34.2	26.6	154.4
2	tap	-	76.0	64.6	53.2	60.0
2	lateral	6.5	44.1	32.7	32.7	72.2

(b)		Approximate depth of electrode (μm)	Atmospheric oxygen composition ^a		
			21% PO ₂ mm Hg	→ 0%	→ 21%
3	tap	10.5	30	107.9	13.7
4	lateral	6.5	30	72.2	15.2
5	tap	7.0	10	66.1	-19.0

Note: a, Remainder of gas composition was nitrogen.

was not accomplished. However, *in vivo* calibration appeared feasible, based on the electrode response to different atmospheric oxygen concentrations, particularly if a suitable system can be developed which will cool the tissue low enough to eliminate aerobic respiration.

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Chapter Thirty-nine

FLOOD TOLERANCE INDICES FOR PALUSTRINE FOREST SPECIES

Russell F. Theriot

INTRODUCTION

Since a definite relationship exists between plant species distribution and timing, frequency and duration of inundation/soil saturation (Bedinger, 1971; Hook and Scholtens, 1978; Whitlow and Harris, 1979; Huffman, 1980; Larson, Bedinger, Bryan, Brown, Huffman, Miller, Rhodes and Touchet, 1981), it should be possible numerically to express the optimum position of various plant species along a wetland hydrologic gradient (Theriot and Sanders, 1986). The resulting numerical values (Flood Tolerance Index) could then be used to estimate the hydrologic regime of areas that have not been substantially altered hydrologically.

Although wetland hydrologic regimes have previously been described in general terms (Cowardin, Carter, Golet and LaRoe, 1979), data needed to define specific hydrologic regimes are seldom available. More specific descriptions of hydrologic regimes were developed for palustrine forests using a zone concept (Clark and Benforado, 1981), in which hydrologic zones were defined on the basis of previous studies. Whereas Clark and Benforado (1981) contains a qualitative list that shows each hydrologic zone in which a species was known to occur, the Flood Tolerance Index (FTI) study numerically describes the ecological amplitude and optimum position of occurrence of plant species along a hydrologic gradient.

Purpose and Objectives

Purpose. The purpose of the study was to develop a concept and method for determining FTI numbers for plant species occurring in palustrine forests of the southeastern United States that are subject to backwater or overbank flooding.

Objectives. Objectives of this research were to develop methods for: (a) translating recorded hydrologic data into hydrologic zone elevations for a particular wetland type; (b) characterizing vegetation in each hydrologic zone; and (c) calculating, verifying and applying FTI numbers.

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Approach

The basic approach was to develop a computer program that used stream gauge data, soil permeability coefficients, and evapotranspiration rates to calculate elevations representing the boundaries of each of six hydrologic zones in palustrine forests of the southeastern United States, based on duration of inundation/soil saturation (Table 39.1). After delineating the hydrologic zones within the study area, the plant species in each hydrologic zone were characterized using standard ecological methods. Resulting values were used to calculate an FTI number for each plant species.

Study Area

The study was conducted in portions of the subtropical ecoregion of the southeastern United States (Bailey, 1976), including portions of eastern Texas and the Gulf and East Coast states (Figure 39.1). Northern limits of the area extended across northern Arkansas, Mississippi and Alabama and included western Florida and all of Georgia and South Carolina except the Piedmont region.

METHODS

Site Selection

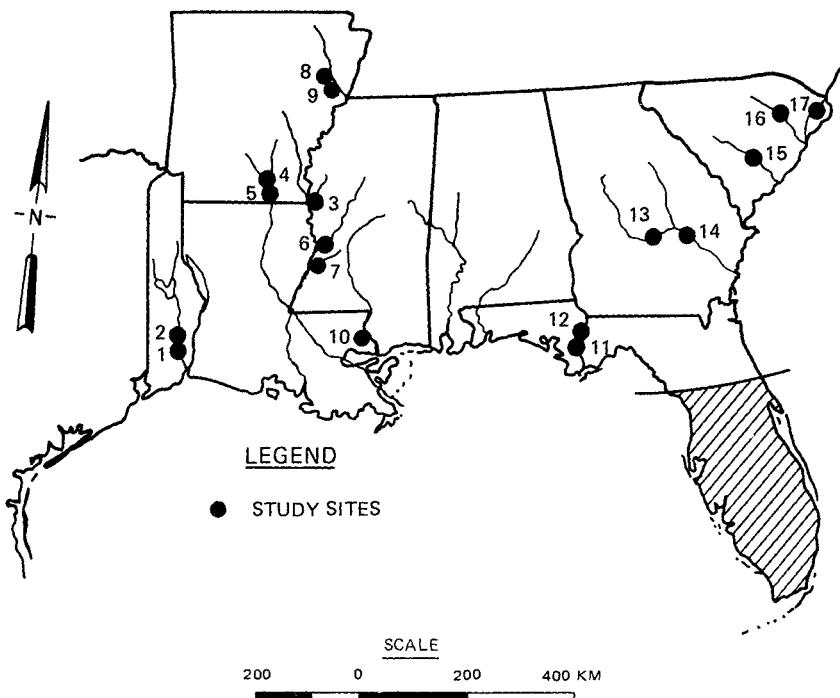
Site selection criteria included:

1. No major disturbance (e.g. recent timber harvesting, ditching, diking) had occurred in the past 20 years.
2. Sufficient hydrologic data (approximately 20 years of daily stream gauge readings) accurately portraying water-level fluctuations on the site (considering ponding, tributary influence between site and gauge, etc.) must be available.
3. No site changes (e.g. timber harvesting, ditching, etc.) anticipated during the study period.
4. Soil data (e.g. soil maps, soil type, texture and permeability coefficients) had to be available.
5. Plant communities had to be characteristic of the area.

Several hundred potential sites were evaluated and most were eliminated due to insufficient stream gauge data. More than 50 sites were visited, but only 17 (Figure 39.1) satisfied all site criteria and were used in the study.

Sites 1 and 2 were on the Neches River in southeastern Texas. Sites 3, 6 and 7 were in Mississippi on Steele Bayou, Yazoo River and Big Black River, respectively. Sites 4 and 5 were on the Ouachita River and Sites 8 and 9 were on the L'Anguille River in Arkansas. Site 10 was on the Pearl River in Louisiana. Sites 11 and 12 were on the Apalachicola River in Florida. Sites 13 and 14 were on the Ocmulgee River and Altamaha river, respectively, in Georgia. Sites 15, 16 and 17 were on the Edisto, Lynches and Waccamaw rivers, respectively in South Carolina.

Figure 39.1: Study area and sites



Determining Hydrologic Zone Elevations

Hydrologic data for each site were obtained either from the United States Geological Survey (flow data) or from the local Corps of Engineer District (stage or flow data). Data were analyzed using a FORTRAN computer program developed for determining hydrologic zone elevations in study sites where flooding occurred. The program output represented the duration of inundation plus soil saturation of each hydrologic zone boundary (Table 39.1), expressed as flow rate or stage data.

Hydrologic zone elevations for each site were computed using the most recent 20 years of daily stream gauge data. When gauge data were provided as daily discharges (flow rate), a rating table (relationship between stage and discharge) was obtained to determine the corresponding stages (elevation).

The dates of the first and last day of the growing season for each site were provided as input to the computer program. The program eliminated all non-growing season data and ranked the remaining daily readings during the 20-year period of record from highest flow (or stage) to lowest. It computed elevations corresponding to the 75, 25, 12.5 and 5 per cent durations of inun-

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Table 39.1: Hydrologic zones occurring in palustrine forests of the Southeastern United States

Zone ^a	Name	Typical inundation/ saturation frequency ^b	Duration ^c
II	Semipermanently to permanently inundated or saturated	Annual (1 yr frequency) 90-100 yr/100 yrs	>75-100
III	Regularly inundated or saturated	51-90 yrs/100 yrs (1 yr-2 yr frequency)	>25-75
IV	Seasonally inundated or saturated	51-90 yrs/100 yrs (1 yr-2 yr frequency)	>12.5-25
V	Irregularly inundated or saturated	11-50 yrs/100 yrs (well drained (>10 yr-2 yr frequency)	5-12.5
		1-20 yr/100 yrs (poorly drained) (100 yr-10 yr frequency)	
VI	Intermittently inundated or saturated	1-10 yrs/100 yrs (100 yr-10 yr frequency)	<5

Notes: a, Zone I, which is open water (aquatic) habitat, was excluded from this study. Zone II is the first wetland zone.

b, Although typical inundation/saturation frequencies for each zone, almost any frequency could be associated with any duration of inundation/saturation. Therefore, only duration of inundation/soil saturation was used to determine hydrologic zones.

c, Duration is based only on the growing season period.

Source: Adapted from Larson *et al.* (1981).

dation. Since the resulting elevations did not include the period during which the soils remain saturated after a period of inundation, it was necessary to integrate saturation effects. A general description of soil types occurring in each zone of the study site were obtained from Soil Conservation Service (SCS) soil surveys. An estimated range of permeabilities for the top 30.5 cm of the soil profile (effective root zone) was then determined. This range approximated the period required for the root zone to become saturated after inundation. The lowest value in the range of permeabilities was used to determine the minimum duration of inundation required to saturate the soil. Another estimated range of soil permeabilities between the 30.5 and 91.5 cm depth was determined. The lowest permeability value of the soil profile between 30.5 and 91.5 cm was used to estimate the time required for desaturation of the root zone after dewatering. A mean daily

transpiration factor for floodplain forests of 5.6 mm (Brown, 1981) was also incorporated.

Permeability and transpiration coefficients were provided as program input, and new flow (or stage) values for hydrologic zone boundaries were derived that reflected both inundation and soil saturation. This iterative process required search by the computer. The computer program added the days of saturation to the days of inundation, and the output was flow (or stage) values that represented the estimated boundary of each hydrologic zone, based on inundation and saturation. The gate datum elevation was added to the stage for each zone to obtain the mean sea level elevation at the gauge. When the site was not immediately adjacent to the gauging station, the change in water surface elevation between the study area and the gauging station was determined using the best available water surface profile data.

Surveying Hydrologic Zone Elevations

A temporary benchmark was established at each of the 17 sites by surveying from a permanent benchmark. Mean sea level elevations for each hydrologic zone boundary were surveyed along the topographic gradient. The contours of each hydrologic zone boundary within the site were marked with surveyor flags. A total of 55 hydrologic zones were established on the 17 study sites.

Selecting Sample Plot Location and Plot Size

Sample plots were established parallel to the hydrologic zone boundary. Plots were positioned on the downslope side of the boundary with at least a 5 m buffer zone maintained between the sample plots and the upper and lower boundary of the hydrologic zone. A belt transect (20 m wide by 40 m long) containing 10 sample plots (8 m by 10 m) was established in each zone.

Vegetation Sampling

The following procedures were used for vegetation sampling:

1. Trees. All trees in each sample plot were identified to species and the diameter; individuals having a diameter of ≥ 7.5 cm at breast height (1.5 m), exclusive of woody vines, were measured and recorded to the nearest whole centimeter.
2. Saplings and shrubs. All samplings and shrubs (woody plants <7.5 cm in diameter, but >1.0 m in height, excluding vines) in each plot were identified to species, and the height class of each individual was recorded. Saplings or shrubs with more than one stem clustered from a single root system were counted as individuals only when separation occurred at or below ground level. The following height classes were used: Class 1 = 1.0-2.0 m; Class 2 = 2.1-3.0 m; Class 3 = 3.1-4.0; Class 4 = 4.1-5.0 m; and Class 5 = >5.0 m.
3. Woody vines. All climbing woody vines >1.0 m in height in each plot were identified to species, the stems of each species were counted, and the height class of the highest individual

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on each tree or sapling/shrub were recorded. The following height classes were used: Class 1 = 1.0-3.0 m; Class 2 = 3.1-6.0 m; Class 3 = 6.1-12.0 m; and Class 4 = >12.0 m. Vines were recorded when any portion of the plant occurred in, or overhung, the plot. Individual stems were recorded when separation from the root system occurred at or below ground level.

4. Herbs and woody seedlings. Percentage cover was estimated for each species of herb and woody seedling (<1.0 m in height) in two randomly located 1.0 m² quadrats in each subplot using the Daubenmire (1968) cover class method.

Analyzing Vegetation Data

Importance values for species in all vegetation layers except the herbaceous layer were calculated by adding values for relative density, relative frequency, and relative dominance. Importance values for herbaceous species were calculated by summing relative frequency and relative dominance. Importance values were used to determine the FTI number for each species.

Calculating Species FTI Numbers

FTI numbers were calculated for each species occurring in each vegetation layer. A species could have three different FTI numbers at a given site, depending on its growth form. For example, Quercus nigra would have three different FTI numbers when present on a site in the tree, sapling, and seedling growth forms. Species FTI numbers for each site were computed by the following formula:

$$FTI_i = \frac{\sum_j (j \cdot IV_{ij})}{\sum_j IV_{ij}}$$

where

i = the ith species

*j = 2.5, 3.5...6.5 (hydrologic zone)

IV_{ij} = importance value for species I in the hydrologic zone j

After species FTI numbers had been computed for all species in all sites, the average FTI number (\bar{FTI}_i) for each species across all sites was calculated using the following formula:

$$\bar{FTI}_i = \frac{\sum_{j=1}^{n_i} FTI_{ij}}{n_i}$$

* Since vegetation was sampled between zone boundaries, mid-range zone values (e.g. 2.5 for Zone II, 3.5 for Zone III, etc.) for zones were used in calculating FTI values.

where

i = the i^{th} species; j = sites 1-17; FTI_{ij} = FTI number
of species i at site j; n_i = number of sites at which species
i occurred.

RESULTS AND DISCUSSION

FTI numbers were computed for 75 tree species, 122 species of saplings and shrubs, 31 species of woody vines, and 264 species of herbs and woody seedlings, representing more than 300 plant species. Separate FTI numbers were derived for the tree, sapling and seedling growth forms of many woody species. FTI numbers of 25 commonly occurring tree species in palustrine forests of the southeastern United States are shown in Table 39.2. Two other systems (wetland indicator status and waterlogging tolerance) for rating the wetness tolerance of palustrine forest species are also shown in Table 39.2. There is general agreement among the three systems. All species having an FTI number from 2 to 4.0 are obligate hydrophytes (OBL) on the National List of Plant Species that Occur in Wetlands (Reed, 1986) and are rated as most or highly tolerant by the waterlogging-tolerance rating (Hook, 1984). All listed species except Pinus taeda that have an FTI number of 6 to 6.5 are facultative upland (FACU) species (Reed, 1986) and are rated by Hook (1984) as the least-tolerant species. P. taeda (FTI-6.41) has an indicator status of facultative (FAC) and is rated as moderately tolerant of waterlogged soils. All species except Betula nigra that have an FTI number of 4 to 6 are facultative wet (FACW) or FAC and are rated as moderately or weakly tolerant. Betula nigra, an OBL species, occurs on well-drained bottomland soils, often on natural berms. FTI numbers were computed only for species occurrence in palustrine forests and do not reflect occurrence in other wetland types (e.g. pocosins, Carolina bays, etc.); thus, slight deviations from the above pattern should be expected for some species.

Example FTI numbers by growth form for woody species are presented in Table 39.3. Although differences between FTI numbers for tree and sapling growth forms are not great, the sapling growth form tends to result in slightly higher FTI numbers because saplings are generally more sensitive to flooding than trees. The sapling growth form also tends to occur in more zones than the tree growth form due to temporal variations in selective pressures (e.g. competition and response to flooding). FTI numbers of seedlings have little value in determining hydrologic zones because they only reflect seed dispersal potential and germination wherever seedbed conditions are favorable. For example, seedlings of intolerant species (e.g. Sassafras albidum) occasionally occur in Zone II, but the individuals do not survive to maturity unless the hydrology is drastically altered.

Ecological amplitudes for selected species based on mean importance values are shown in Figure 39.2. Since the FTI num-

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Table 39.2: A comparison of three water-tolerance ratings for selected palustrine forested species

Species	FTI ^a ± Sd	NWI ^b status region 2	Waterlogging tolerance rating group ^c
<i>Nyssa aquatica</i>	2.62 ± 0.20	OBL	Most
<i>Cephalanthus occidentalis</i>	2.83 ± 0.52	OBL	Most
<i>Salix nigra</i>	2.83 ± 0.58	OBL	Most
<i>Fraxinus caroliniana</i>	2.87 ± 0.41	OBL	Most
<i>Taxodium distichum</i>	2.97 ± 0.61	OBL	Most
<i>Forestiera acuminata</i>	3.48 ± 0.50	OBL	Most
<i>Gleditsia aquatica</i>	3.50 ± 0.00	OBL	Highly
<i>Carya aquatica</i>	3.45 ± 0.34	OBL	Highly
<i>Quercus lyrata</i>	3.73 ± 0.68	OBL	Highly
<i>Betula nigra</i>	4.01 ± 1.73	OBL	Moderately
<i>Diospyros virginiana</i>	4.13 ± 0.82	FAC	Moderately
<i>Acer rubrum</i>	4.21 ± 0.68	FAC	Moderately
<i>Fraxinus pennsylvanica</i>	4.44 ± 0.67	FACW	Moderately
<i>Ulmus americana</i>	4.46 ± 0.62	FACW	Moderately
<i>Quercus phellos</i>	4.81 ± 1.07	FACW	Moderately
<i>Carpinus caroliniana</i>	4.84 ± 0.61	FAC	Weakly
<i>Celtis laevigata</i>	4.84 ± 0.56	FACW	Weakly
<i>Acer negundo</i>	4.88 ± 0.47	FACW	Moderately
<i>Liquidambar styraciflua</i>	5.03 ± 0.65	FAC+	Moderately
<i>Carya illinoensis</i>	5.57 ± 1.01	FAC+	Weakly
<i>Pinus taeda</i>	6.41 ± 0.14	FAC	Moderately
<i>Cornus florida</i>	6.50 ± 0.00	FACU	Least
<i>Fagus grandifolia</i>	6.50 ± 0.00	FACU	Least
<i>Quercus alba</i>	6.50 ± 0.00	FACU	Least
<i>Sassafras albidum</i>	6.50 ± 0.00	FACU	Least

Notes: a, Mean for all study sites.

b, Taken from Reed (1986), see Appendix A.

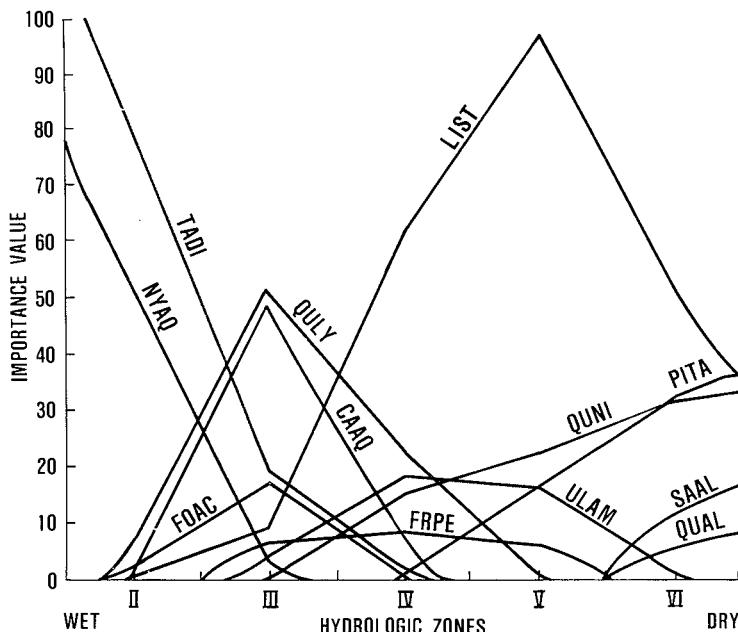
c, Taken from Hook (1984), see Appendix B.

bers were calculated from mean importance values and not the maximum important value obtained for each species, they do not represent the maximum in ecological amplitude. Three patterns are shown in Figure 39.2. The first group includes species such as *Nyssa aquatica* and *Taxodium distichum*, in which mean importance value is greatest in Zone II and the species no longer occurs after either Zone III or IV. This pattern is indicative of species having the strongest competitive advantage in areas of greatest duration of inundation/soil saturation. The second group is typified by species such as *Quercus nigra*, *Pinus taeda*, *Sassafras albidum* and *Quercus alba*, in which the greatest mean importance value occurs in Zone VI (uplands) and decreases from Zone V to II. Hence they have a stronger competitive advantage in areas where inundation/

Table 39.3: Flood tolerance index by growth form

Scientific name	Tree	Sapling	Seedling
<u>T.distichum</u>	2.97	3.33	3.09
<u>C.aquatica</u>	3.50	3.15	3.27
<u>C.aquatica</u>	3.54	3.70	3.69
<u>Q.lyrata</u>	3.73	3.99	3.80
<u>F.pennsylvanica</u>	4.44	4.27	4.00
<u>Q.nuttallii</u>	4.50	4.50	4.50
<u>A.negundo</u>	4.83	5.20	5.58
<u>C.laevigata</u>	4.84	4.37	4.77
<u>L.styraciflua</u>	5.03	5.52	4.87
<u>Q.nigra</u>	5.73	5.92	5.85
<u>S.albidum</u>	6.50	6.50	6.07

Figure 39.2: Ecological amplitude of some commonly occurring species. TADI: Taxodium distichum; NYAQ: Nyssa aquatica; QULY: Quercus lyrata; FOAC: Forestiera acuminata; CAAQ: Carya aquatica; LIST: Liquidambar styraciflua; FRPE: Fraxinus pennsylvanica; QUINI: Quercus nigra; ULAM: Ulmus americana; PITA: Pinus taeda; SAAL: Sassafras albidum; QUAL: Quercus alba



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soil saturation is less than 5 per cent of the growing season. However, some of these species (e.g. Quercus nigra and Pinus taeda) may occasionally occur as dominants in wetlands. The third group is typified by species having greatest mean importance values in Zones III-V. Species in this group sometimes occur as dominant species in either Zone II or VI, but are best adapted for occurrence at some point in Zones III-V. Species having greatest mean importance values in Zone III are Quercus lyrata and Carya aquatica, while Ulmus americana and Liquidambar styraciflua develop greatest mean importance values in Zones IV and V, respectively.

CONCLUSIONS

1. Elevations of hydrologic zones of palustrine forests can be determined by analyzing gauging station data.
2. FTI numbers can be calculated that reflect the position of optimal occurrence of plant species along the hydrologic gradient.
3. Calculated FTI numbers are in general agreement with other systems for describing wetness tolerance.
4. Plant species occurring in palustrine forests of the southeastern United States demonstrate one of three distinctive patterns with reference to ecological amplitude.

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APPENDIX A

Definitions for NWI Status Descriptors

Obligate (OBL). Always found in wetlands under natural (not planted) conditions (frequency greater than 99 per cent), but may persist in non-wetlands if planted there by man or in wetlands that have been drained, filled, or otherwise transformed into non-wetlands.

Facultative Wetland (FACW). Usually found in wetlands (67-99 per cent frequency), but occasionally found in non-wetlands.

Facultative (FAC). Sometimes found in wetlands (34-66 per cent frequency), but also occurs in non-wetlands.

Facultative Upland (FACU). Seldom found in wetlands (1-33 per cent frequency) and usually occurs in non-wetlands.

Non-wetland (UPL). Occurs in wetlands in another region, but not found (<1 per cent frequency) in wetlands in the region specified. If a species does not occur in wetlands in any region, it is not on the list.

A positive (+) or negative (-) symbol was used with the Facultative Indicator categories to define more specifically the regional frequency of occurrence in wetlands. The positive sign indicates a frequency toward the higher end of the category (more frequently found in wetlands), and a negative sign indicates a frequency toward the lower end of the category (less frequently found in wetlands).

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APPENDIX B

Definitions for Waterlogging Tolerance Rating

Most Tolerant. Those species that are capable of living from seedling to maturity in soils that are waterlogged almost continually year after year except for short durations during droughts. The soils are typically anaerobic in character but are less so where the water is moving. Some species in this group adapt by producing soil water roots that oxidize their rhizosphere, accelerate anaerobic metabolism but at a controlled rate and tolerate the toxic compounds typical of highly reduced waterlogging soils.

Highly Tolerant. Those species capable of living from seedling to maturity in soils that are waterlogged for 50 to 75 per cent of the year. Waterlogging typically occurs during the winter, spring and 1-3 months of summer.

Moderately Tolerant. Those species capable of living from seedling to maturity in soils waterlogged about 50 per cent of the time. Waterlogging typically occurs in portions of the winter, spring, and early summer.

Weakly Tolerant. Those species that are capable of living from seedling through maturity in soils that are temporarily waterlogged for durations of 1-4 weeks and usually accounting for 10 per cent of the growing season.

Least Tolerant. Those species that are capable of living from seedling through maturity in soils that are occasionally waterlogged for durations of a few days only, usually accounting for less than 2 per cent of the growing season.

Chapter Forty

INTERSPECIFIC GENETIC VARIATION OF LOBLOLLY PINE TOLERANCE TO SOIL WATERLOGGING

Theodore H. Shear and Donal D. Hook

INTRODUCTION

Loblolly pine (*Pinus taeda*) is the most important commercial tree in the southern United States. It attains maximum size and growth rate on moderate to wet sites adjacent to wetlands (i.e. swamps and river bottoms). Individual trees grow in headwater swamps and other shallowly inundated wetlands. Hence, there is evidence of interspecific variation in tolerance to waterlogging.

Many wet sites in the South planted with loblolly pine require bedding, surface drainage, and phosphorus fertilization in order to obtain acceptable survival and growth (numerous studies have shown that tolerance of loblolly pine to waterlogging on some soils can be increased by adding phosphorus). Major tree improvement programs have not selected for waterlogging tolerance, except for one industrial seed orchard in North Carolina. Hence, no known waterlogging-tolerant genotypes of tree species have been identified or developed. If more-tolerant genotypes could be identified or bred, many acres of marginal productive wet pine sites could be hand planted with tolerant progeny and fertilized with phosphorus, resulting in increased productivity with minimal site disturbance.

Our objectives were to determine (1) if significant interspecific variability in resistance to waterlogging occurred, (2) if the variability was sufficiently large to have practical application, and (3) if physiological measures of waterlogging tolerance could be used for progeny selection. This chapter reports on research in progress to meet these objectives.

METHODS AND MATERIALS

Eleven seed sources (ten open-pollinated families and one general coastal plain source) were planted in soil tanks (Hook, Langdon, Stubbs and Brown, 1970) and on three different field sites in June 1984. Soil tanks were either continuously flooded or seasonally flooded. For each treatment, twelve trees of each source were planted in three different tanks. Field sites varied from moderately wet to very wet. All were waterlogged during the winter (wet site, 0-15cm standing water; wetter, 0-30cm; wettest, 0-45cm). All sites

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Table 40.1: Analysis of variance of progeny tests. Volume is the dependent variable in each analysis (volume = diameter² x height)

		Mean square	F ratio	P
<u>Wet site</u>	$r^2 = 0.094$			
	water depth	605691	6.406	0.012
	source	1825734	1.931	0.042
	error	94553		
<u>Wetter site</u>	$r^2 = 0.138$			
	water depth	3989365	18.758	0.000
	source	3486889	1.640	0.098
	error	212671		
<u>Wettest site</u>	$r^2 = 0.260$			
	water depth	631239	71.044	0.000
	source	22509	2.533	0.006
	error	8885		

dry during the growing season such that the water table at the wettest site may recede to several inches below the soil surface.

At the wet site, two blocks with four replications each were planted. Each replication contains one row of each seed source. Each row contains seven trees and occurs randomly in the replication. At the wetter site, two blocks with two replications were planted. At the wettest site, five sets of each source, each containing seven seedlings, were planted in eleven rows in one block.

The height and diameter of each seedling were measured annually. The depth of the water table (above or below the soil surface) was measured seasonally by the rusty rod method of McKee (1978). A mild steel rod was placed in the ground next to each tree and removed eight weeks later. That part of the rod in waterlogged soil (or standing water above the ground) did not rust while the rest of the rod rusted in an aerobic environment. This provided a measure of the water table at each microsite.

RESULTS AND DISCUSSION

After two years, significant differences were apparent with the wettest treatments (Figures 40.1 and 40.2). In other treatments, while mean volumes were not significantly different, some sources had individuals that excelled on wet sites while others did not. In the field tests, as much as 20 per cent of the variation in volume was dependent on water-table level. Approximately 7 per cent was attributable to seed source (Table 40.1). These results were comparable to those of many tree progeny tests.

Figure 40.1: Means and ranges of volume of eleven families growing in soil tanks with two flooding regimes, determined at the end of the second growing season. Families underscored by the same line were not determined to be significantly different by Tukey's studentized range test ($\alpha = 0.05$).

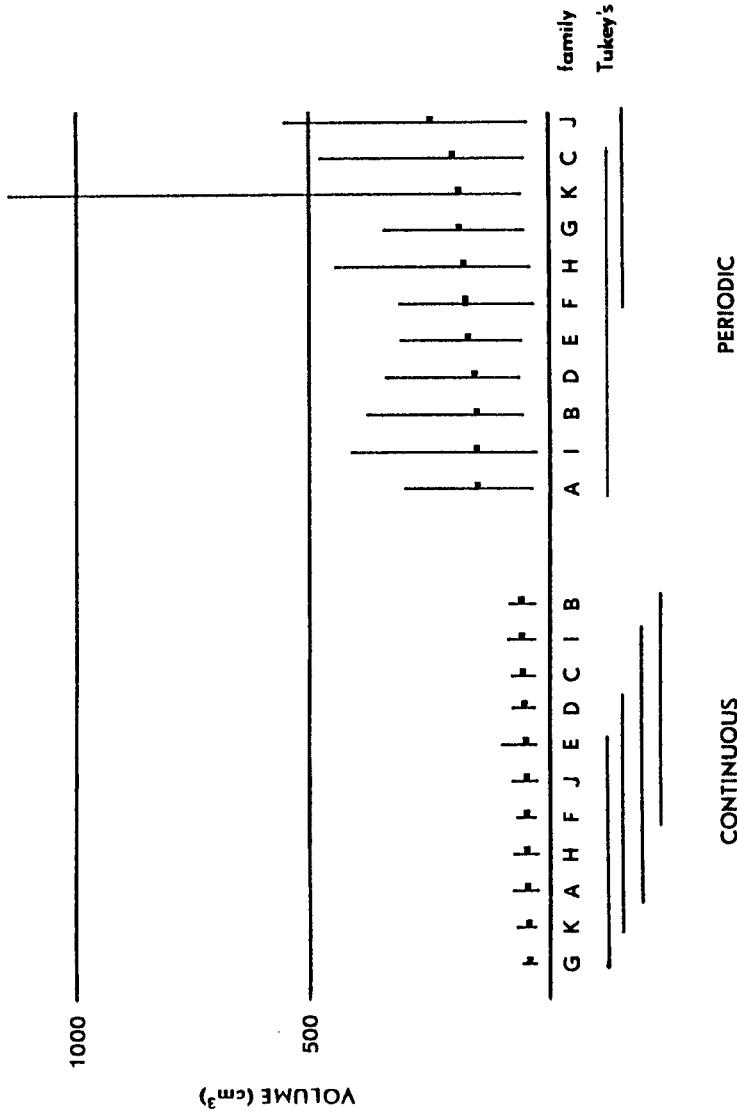
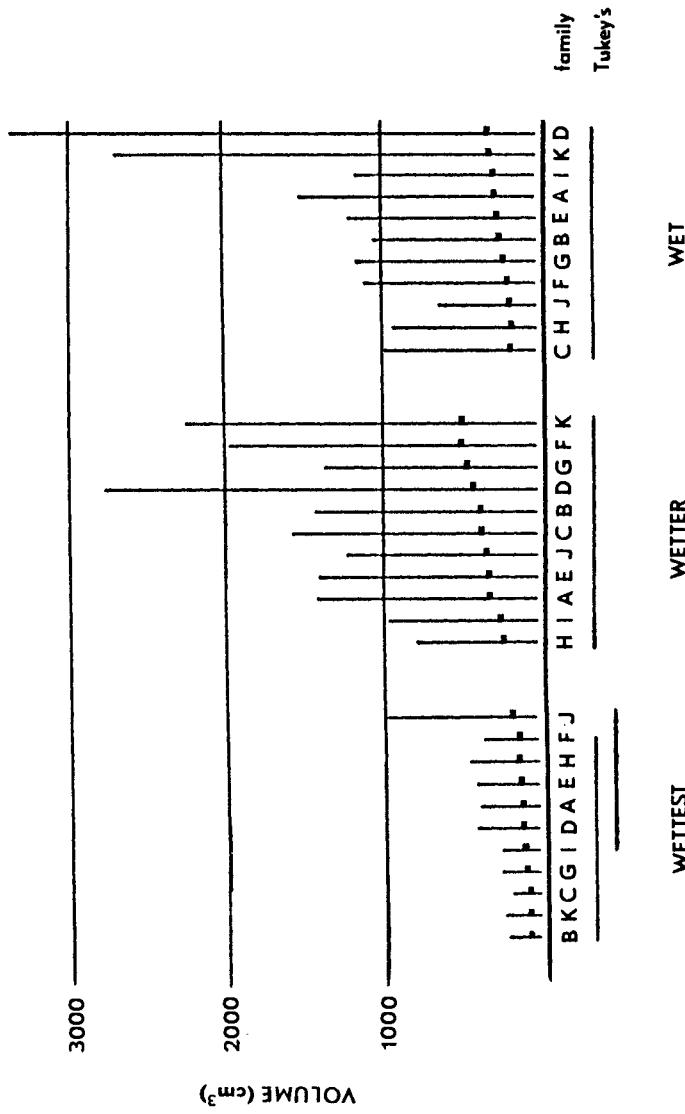


Figure 40.2: Means and ranges of volume of eleven families growing on three different wet sites, determined at the end of the second growing season. Families underscored by the same line were not determined to be significantly different by Tukey's studentized range test ($\alpha = 0.05$).



The results of the soil tank tests will be correlated with long-term results of the field tests to see if controlled intense waterlogging can predict field performance. The seedlings in the tanks will be harvested in late summer 1986 and analyzed for differences in anaerobic metabolism, anatomy, internal aeration, alcohol dehydrogenase activity, and growth analysis measures. Prior results with year-old seedlings showed that anaerobic metabolism traits varied among families, but growth differences were too small to be correlated with tolerance mechanisms (Hook and Denslow, 1986).

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PART VI

ESTUARINE WETLANDS AND INTERACTIONS AMONG THEIR COMPONENTS

Chapter Forty-one

PATHWAYS AND CONTROLS OF THE CARBON CYCLE IN SALT MARSHES

James T. Morris

INTRODUCTION

It is argued that intertidal wetlands are a necessary link in coastal food chains and that their protection is vital to the continued productivity of coastal marine fisheries (Teal, 1962; Teal and Teal, 1969; Odum, 1971; Gosselink, Odum and Pope, 1974). These arguments have apparently been persuasive among legislators. Several states, including South Carolina, have established a permitting process, through provisions in the Federal Coastal Zone Management Act, designed to protect intertidal wetlands. Current legislation, however, fails to take into account the dynamic nature of intertidal ecosystems.

Geological evidence (Redfield and Rubin, 1962; Gardner and Bohn 1980; Jaworski and Tedrow, 1985) indicates that there is presently a landward migration of salt marsh communities in response to local sea level rise. The present rate of sea level rise along the South Carolina coast is 3.6 mm/yr based upon tide gauge recordings in Charleston Harbor (Hicks and Crosby, 1974). This rate could accelerate, with sea level rising 5 - 6 m in a century or less if current predictions about a global warming trend are correct (Mercer, 1978; Hansen, Johnson, Lacis, Lebedeff, Lee, Rind and Russell, 1981). Even a significantly lower rate would have a large impact on intertidal wetland communities. It is likely that coastal dikes would be constructed to prevent flooding and this could threaten the existence of intertidal communities as we now know them. It may be desirable to develop management schemes that allow salt marsh habitats to migrate. It also seems prudent that we should intensify efforts to expand our basic understanding of the structure and function of these ecosystems. In this chapter I highlight some of the research that deals with the pathways of carbon movement and control mechanisms of the carbon cycle in salt marshes.

STRESS GRADIENTS AND SPARTINA GROWTH

While the lower elevations of the east coast salt marshes are dominated by a nearly pure monoculture of Spartina alterniflora, they are hardly uniform in productivity. They invariably contain gradi-

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ents of productivity that form along stress gradients and that are easily identified on the basis of the height of the Spartina grass. S. alterniflora is tallest and most productive near the banks of tidal creeks and decreases in stature and productivity with increasing distance from the creeks. The upland limit of S. alterniflora is characterized by the appearance of other plant species. In southeastern marshes, Juncus roemerianus is the dominant vegetation at the transition between upland vegetation and Spartina marsh. Juncus has wide environmental tolerances in comparison to other tidal marsh angiosperms and is adapted to a zone characterized by extreme variations in physical variables, including salinities that may rise to 90-360 ppt (Eleuterius, 1984). From North Carolina to New England Spartina patens dominates this transition zone in the high marsh and shows a considerable degree of phenotypic and genotypic plasticity (Silander, 1979, Silander and Antonovics, 1979).

A great deal of research from the past decade is related to the nature of these stress and productivity gradients. Early research implicated nitrogen limitation as a cause of the reduced productivity of Spartina in the high marsh (Sullivan and Daiber, 1974; Valiela and Teal, 1974; Broome, Woodhouse and Seneca, 1975; Gallagher, 1975; Patrick and DeLaune, 1976). Drainage, pore water movement, sediment aeration, redox potential and sulfide concentration have also been implicated in regulation of Spartina productivity (Mendelsohn and Seneca, 1980; Mendelsohn, McKee and Patrick, 1981; Howes, Howarth, Teal and Valiela, 1981; Linthurst, 1980b; Linthurst and Seneca, 1980; Wiegert, Chalmers and Randerson, 1983; King, Klug, Wiegert and Chalmers, 1982; DeLaune, Smith and Patrick, 1983). Soil redox state and nitrogen availability are related because nitrogen uptake by Spartina is controlled by the availability of oxygen to the roots (Morris and Dacey, 1984). There is also evidence that sulfides inhibit nutrient uptake by a number of salt marsh plants (Ingold and Havill, 1985), although I will discuss results below that suggest that sulfide levels may not be of great importance in at least one site in South Carolina.

High salinity has also been shown to reduce the growth of Spartina spp. (Phleger, 1971; Smart and Barko, 1978; Linthurst, 1980a; Webb, 1983; Pearcy and Ustin, 1984), and soil salinity in the high marsh zone often increases to levels greater than sea water (e.g. Gardner, 1973). This finding relates to the observations about the effects of nitrogen availability and soil redox state, because of the influence of nitrogen on the accumulation of osmotica in Spartina. It is thought that Spartina uses the free amino acid proline and quaternary ammonium compound glycine-betaine to osmoregulate (Cavalieri and Huang, 1979). As much as 19 to 30 per cent of the total leaf nitrogen may be in the form of these compounds in the leaves of short (stressed) Spartina plants (Cavalieri and Huang, 1981), and the accumulation of both are sensitive to nitrogen availability (Cavalieri, 1983). Thus, nitrogen stress may lead to a breakdown in the ability of the plant to osmoregulate. This is supported by observations that short Spartina from the high marsh has a lower water use efficiency (Giurgevich and Dunn, 1979, 1982), lower turgor pressure (Drake

and Gallagher, 1984), and higher leaf temperatures (Shea, 1977) than the more productive plants that are located along the creek banks.

It has also been proposed that there may be a positive feedback between Spartina growth and sediment oxidation (Howes, Howarth, Teal and Valiela, 1981; Dacey and Howes, 1984; Morris and Whiting, 1985), since sediment oxidation is a function of evapotranspiration rate and air entry into the sediment. For example, Morris and Whiting (1985) found that as much as 4 L/m^2 of air was drawn into the sediment during low tide as the water-table dropped. In the high marsh, water-table movements appear to be determined by the amount of water lost by evapotranspiration. It follows, that as biomass and transpiration increases, then the amount of air drawn into the sediment should also increase. However, water use data we have derived from experimental marsh mesocosms challenge the assumption that total evapotranspiration increases in proportion to primary production in waterlogged sediments.

Our data indicate that evaporation from a saturated sediment without vegetation is as great as total evapotranspiration from a vegetated salt marsh sediment. Ten 1 m^2 experimental marsh mesocosms containing 30 cm of sediment were established in early 1985. Eight mesocosms contained vigorous populations of S. alterniflora while two were non-vegetated. At least four times a week beginning June 1984, we recorded the quantity of water that was added to each mesocosm in order to bring the water-table level to the sediment surface. Both the pattern and magnitude of daily water use in the vegetated and non-vegetated mesocosms were strikingly similar. Mean water use in the non-vegetated and vegetated mesocosms were not significantly different and averaged 2.21 and 1.95 $\text{L m}^{-2} \text{ day}^{-1}$, respectively, from June to September (Table 41.1). Highest rates of evapotranspiration during this period were observed during September when the vegetated mesocosms used 3.03 $\text{L m}^{-2} \text{ day}^{-1}$ and the non-vegetated mesocosms used 3.79 $\text{L m}^{-2} \text{ day}^{-1}$. These rates are consistent with the measurements of air entry into the sediment (Morris and Whiting, 1985). Apparently, in a waterlogged sediment the rate-limiting factor for transfer of water to the air is the sink, which is determined by the difference between the vapor pressure of the atmosphere and the saturated vapor pressure. The highest rate of water movement to the air is not from any vegetated landscape, but from open ocean where it can exceed 300 cm/y (Brutsaert, 1982).

We have conducted an experiment designed to test the effect of lowering the ambient sulfide levels on growth of Spartina in the high marsh at the Goat Island site (Figure 41.1) in North Inlet. A total of 30 mol/m² of ferric iron as goethite was added to the sediments of six experimental plots at one time in April, 1984 in order to precipitate the sulfides. We also began fertilizing plots biweekly with 1.37 mol N/m² as NH₄Cl; the nitrogen treatment was applied to six plots, including three of the plots that had been treated with iron. Beginning in the spring of 1985 we began fertilizing iron-treated plots and three disturbed control plots with phosphate. Biweekly additions of 0.69 mol P/m² as KH₂PO₄ were applied to disturbed controls and iron-only treated plots, and 1.37

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Table 41.1: Mean daily water use (± 1 SD) by month from experimental marsh mesocosms containing bare sediment only or planted with Spartina alterniflora

	June	July	August	September	Mean daily water use ($1 \text{ m}^{-2} \text{ day}^{-1}$) All dates
Vegetated	1.45 ± 0.86	1.06 ± 0.94	1.88 ± 1.59	3.03 ± 1.42	1.95 ± 1.53
Non-vegetated	2.53 ± 2.77	1.01 ± 1.2	1.78 ± 2.24	3.79 ± 2.33	2.21 ± 2.36

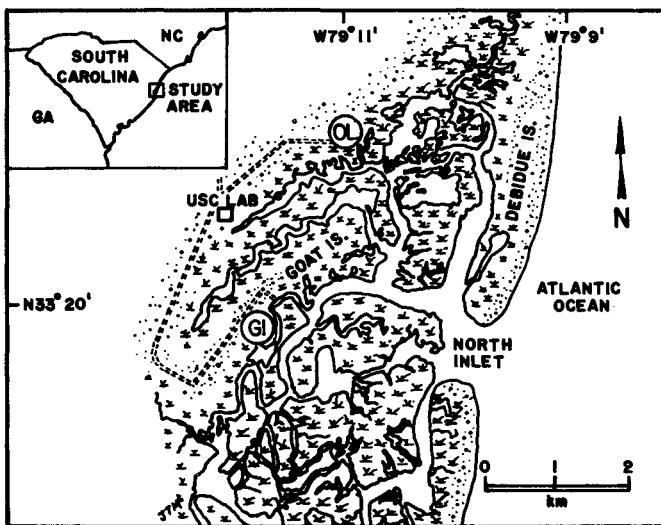
mol N/m² and 0.69 mol P/m² as $(\text{NH}_4)_2\text{HPO}_4$ (instead of NH₄Cl) was applied biweekly to the three plots treated with a combination of iron and nitrogen. The results have indicated that the iron treatment, which did effectively lower the sulfide concentrations (G.M. King, unpublished data), had no effect on growth (Figure 41.2). These results also confirm the importance of nitrogen availability and the insignificance of phosphorus, since the growth response to nitrogen was immediate and dramatic while there was no response in the disturbed control treatment to phosphate (Figure 41.2).

Another conclusion we can make from these data is that interannual variability in aboveground growth is quite high. For example, in the undisturbed control plots, aboveground biomass peaked at 241 g dry wt/m² during the 1984 growing season and 647 g/m² during the 1985 growing season (Figure 41.2). The same increase in biomass was observed during 1985 in all the experimental plots. There was also a concurrent increase in stem density by approximately a factor of 2. There is no possibility that these differences are due to spatial variability within the marsh and sampling error, because biomass was measured non-destructively on permanent plots by taking a monthly census of stem heights and applying a regression equation to obtain the stem dry weight. The reason for these differences in annual growth is unknown. Annual rainfall during both years was approximately 72 cm and the pattern of rainfall (Figure 41.3) does not suggest that this could be a factor. Interannual variations of productivity might be caused by a number of factors. They include annual variations in sea level, which can be as great as 10 cm (Kjerfve, Greer and Crout, 1978). This could affect sediment salinity and other aspects of pore water chemistry. There may even be intrinsic cycles that operate on the basis of negative feedback, such as a cycle of high productivity one year followed in the next year by a high degree of standing dead biomass and self-shading.

ACROSS GRADIENT COMPARISONS

We have some comparative data on primary production and CO₂ exchanges across a stress gradient at a site known as Oyster Landing (OL) in the North Inlet estuary of South Carolina (Figure

Figure 41.1: Location of study areas Oyster Landing (OL) and Goat Island (GI) within the North Inlet estuary



41.1). They include summaries of CO₂ diffusion from the marsh sediment (Morris and Whiting, 1986), gross photosynthesis, and total ecosystem respiration (Table 41.2). Total sediment organic matter and root biomass were similar among creek bank (low stress) and high marsh (high stress) sites at OL (Figures 41.4 and 41.5). Total annual CO₂ diffusion from the marsh sediment is lower at the creek bank site, although total ecosystem respiration, gross photosynthesis and biomass are higher (Table 41.2).

The response of an ecosystem to stress, termed a retrogression by Whittaker (1975), is thought to include a reduction in those properties that tend to increase through successional time, such as productivity and biomass. While we do see a decrease in biomass and primary production with increased stress, we did not see a change in the ratio of GPP/R; the latter were 0.81–0.85 (Table 41.2). When total respiration was partitioned between aboveground respiration and soil respiration, there was a trend toward a relative increase in the amount of aboveground respiration at the tall site consistent with the increase in aboveground biomass. It is disturbing that the ratios of GPP/R were <1 at these sites; this is not what one would expect of any ecosystem that is thought to be accumulating organic matter. This result could be due to errors associated with the integration of the empirical measurements of gross photosynthesis and respiration, or it could indicate that there was a net import of organic matter at this site. It is also possible that annual rates of ecosystem respiration and

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Figure 41.2: Biomass of Spartina alterniflora in control plots and within plots treated with iron, nitrogen, and a combination of iron and nitrogen. All plots are within the same general area characterized by short Spartina at the Goat Island site

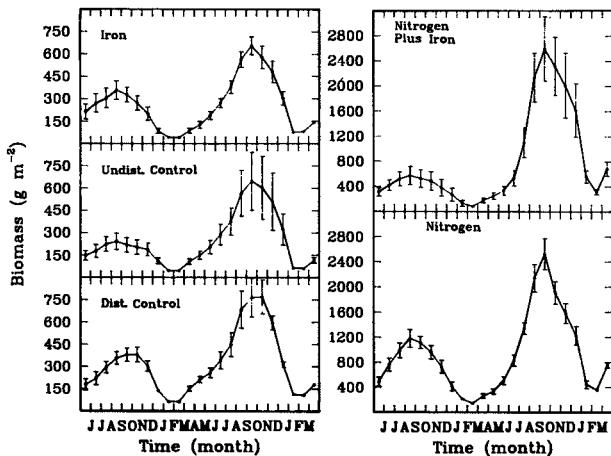
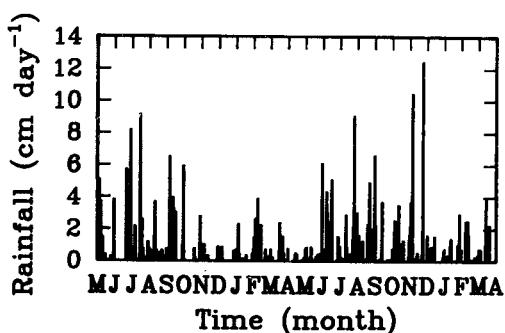


Figure 41.3: Daily rainfall totals at the North Inlet estuary during the study beginning May 1984 and ending April 1986



gross photosynthesis may vary independently or out of phase of one another. If this is correct, then conclusions about the metabolic status of a marsh made from a single year of data will be difficult to make.

Table 41.2: System level characteristics across a stress gradient in a North Inlet salt marsh at Oyster Landing (OL); units of biomass, respiration and gross photosynthesis are moles C m⁻² or moles C m⁻² yr⁻¹

	Site	
	OL short	OL tall
Characteristics		
Maximum live aerial biomass ^a	16	47
Live belowground biomass ^b	34	32
Stem density (m ⁻²) ^a	366-606	119-355
Yearly ecosystem respiration (R) ^c	61	123
Total yearly soil respiration ^{b,c}	30	22
Total yearly GPP ^d	52	100
GPP/R	85%	81%
soil resp/GPP	57%	22%

Notes: a, Maximum biomass and range in stem density for the period July 1983 to July 1984.

b, Morris and Whiting (1986).

c, Annual ecosystem and soil respiration estimated from monthly measurements made with chambers.

d, Annual GPP estimated from monthly measurements with chambers, and integrated using a model of photosynthesis (Morris, 1982; Morris et al., 1984)

ECOSYSTEM PROPERTIES AS FUNCTIONS OF MARSH AGE

The age of a particular salt marsh is one important and often overlooked variable that affects the structure and function of marsh ecosystems. Stratigraphic and aerial maps of the North Inlet estuary in South Carolina reveal that the salt marshes here are colonizing the valleys between old beach ridges as sea level rises (Gardner and Bohn, 1980). A hypsometric curve of the innermost basin to the west, known as Ely Creek, suggests that this is an immature marsh which has not yet reached equilibrium (Eiser and Kjerfve, 1987). This chronology of marshes of varying age arises because of rising sea level, as discussed above. Sedimentation rates within this salt marsh vary from 1.4 to 2.4 mm/yr or more depending on location, based on ²¹⁰Pb profiles (Gardner, Sharma and Moore, 1986). Therefore, these marshes appear capable of accumulating sediment at a rate that is equal to the present rise in sea level while new marsh habitats migrate inland. Along the South Carolina coast the upland areas behind the salt marshes are classified as pine savanna. Soils in the pine savanna are low in organic matter content, and have a mineral composition that is high in sand (81 per cent), and low in silt (13 per cent) and clay (6 per cent) (Jones and Gresham, 1985). On the basis of the differences in soils among young colonizing marshes and those on deep

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Figure 41.4: Depth profiles in sediment of total organic matter, measured as percentage dry weight loss after ignition, at Goat Island sites characterized by tall and short Spartina alterniflora (GI-T and GI-S, respectively) and at Oyster Landing sites with tall and short Spartina (OL-T and OL-S)

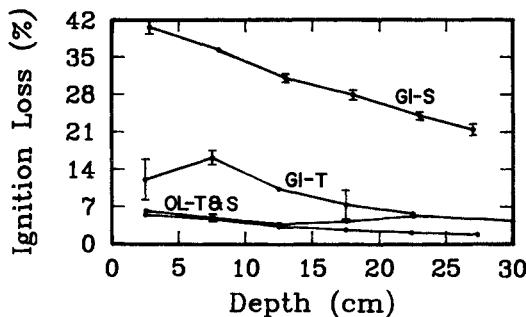
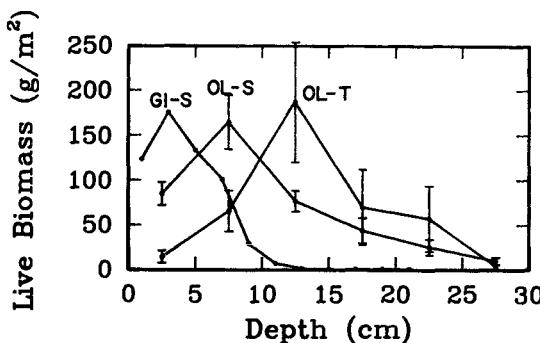


Figure 41.5: Depth profiles in sediment of total live biomass at the Goat Island short Spartina site (GI-S) and Oyster Landing tall and short Spartina sites (OL-T and OL-S)



posites of silt and peat, one could expect differences in productivity as well as quantitative differences in other aspects of the carbon cycle.

Marsh locations where we have some comparative data are indicated on the map (Figure 41.1) as OL (Oyster Landing) and GI (Goat Island). The OL site is the younger of the two. A ^{210}Pb profile from a high marsh site at OL (Figure 41.6) is characteristic of a non-depositional environment; the soil here is sandy and is part of the beach ridge complex that only recently has been colonized by marsh vegetation. The ^{210}Pb profile from the high marsh at Goat Island is characteristic of a depositional environment and shows evidence of bioturbation near the surface (Figure 41.6). Depth profiles from the short Spartina zones at OL and GI show

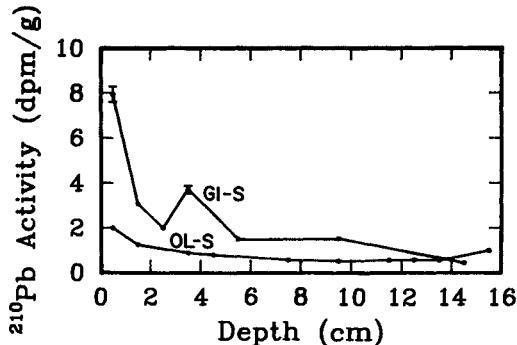
that the accumulation of sediment organic matter (SOM) at the GI site is much greater than at OL (Figure 41.4), which is consistent with the notion that organic matter accumulates in marsh ecosystems as they mature. However, total live root and rhizome biomass at the two sites is similar (considering errors involved in measuring belowground biomass): 408 and 575 g/m² at OL and GI, respectively.

There does appear to be a shift in the position of maximum, live belowground biomass toward the surface in the environments that we would expect to have the lower redox potentials. For example, the peak belowground biomass is deepest at the creek-bank site at OL; it shifts towards the surface at the short Spartina zone at OL, and is nearest to the surface at the short Spartina zone at GI (Figure 41.5). This may indicate that the roots are forced to the surface, toward the oxygen source, as a consequence of decreasing redox potential. Sediment redox potential is a function of distance from tidal creek (Howes, Howarth, Teal and ValIELA, 1981; Mendelsohn, Makee and Patrick, 1981) and possibly marsh age as well, since organic matter accumulation is a function of time.

It is difficult to find comparative data on trends in ecosystem respiration, gross photosynthesis, or net ecosystem production across age or stress gradients in salt marshes. CO₂ flux from sediments at the GI short Spartina site appear to be greater than from the younger OL short Spartina site. During August, 1985, CO₂ diffusion rates from the sediment surface at OL and GI were 34±13 and 100±34 ml CO₂ m⁻² h⁻¹, respectively. Thus, total heterotrophic metabolism may be greater in the mature marsh. Across stress gradients, Blum, Seneca and Stroud (1978) found that total ecosystem respiration increased from 65 to 71 per cent of total gross photosynthesis along a transect from short to tall Spartina. In this North Carolina marsh, soil respiration accounted for the largest amount of ecosystem respiration in short Spartina sites, and aboveground respiration accounted for the largest amount of ecosystem respiration in tall Spartina sites. These trends are consistent with our observations at Oyster Landing. Drake and Read (1981) measured CO₂ exchanges at a single marsh site in Maryland and reported a net daylight uptake of 62 mol C/m² and a loss at night of 36 mol/m² for the period April to December. Only net daytime uptake and nocturnal respiration rates were reported. Annual CO₂ loss from sediments of a Louisiana salt marsh was 34.8 mol/m² (Smith, DeLaune and Patrick, 1983) and is the major carbon output from net primary production there (Feijtel, DeLaune and Patrick, 1985). Houghton and Woodwell (1980) found that annual aboveground plant respiration was 60 per cent of GPP, which was estimated to be 72 mol/m², in Flax Pond marsh. Teal (1962) concluded that plant respiration in a Georgia marsh was 77 per cent of GPP and that microbial respiration accounted for 47 per cent of the remainder. Newell, Fallon, Rodriguez and Groene (1985) concluded that the CO₂ production from decomposition of standing dead litter in the tall Spartina zone exceeds the benthic oxygen demand, whereas the relative rates of benthic metabolism and aboveground decomposition are reversed in the short zone.

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Figure 41.6: Depth profiles in sediment of ^{210}Pb activity on short Spartina sites at Goat Island (GI-S) and Oyster Landing (OL-S)



This survey of ecosystem level metabolic patterns across age and stress gradients is tentative at best, because the annual variability and coupling between total ecosystem respiration and gross photosynthesis are unknown. Biomass data from the GI short Spartina site shows that interannual variation in aboveground production can be large (Figure 41.2). Since belowground organic matter has a decomposition time exceeding 1 yr (Hackney and de la Cruz, 1980; Van der Valk and Attiwill, 1983; Valiela, Wilson, Buchsbaum, Rietsma, Bryant, Foreman and Teal, 1984), sediment metabolism is buffered to some extent against variations in primary production. Interannual variations in total gross photosynthesis and its partitioning between plant respiration, aerobic and anaerobic microbial respiration, and export, need to be quantified.

CONCLUSIONS

Productivity of Spartina alterniflora along stress gradients in salt marshes is governed by a complex interaction among variables that include nitrogen availability, sediment oxidation, hydrology, and salinity. The greatest sink for gross photosynthesis is plant respiration, the greatest sink for net plant production appears to be heterotrophic metabolism within the sediments. Beyond this, it is presently difficult to generalize about trends in carbon metabolism in marshes because of differences among marsh sites in level of stress and age. Marshes of different ages develop because of rising sea level and appear to show quantitative differences in carbon cycling.

ACKNOWLEDGEMENTS

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Chapter Forty-two

IRREGULARLY FLOODED SALT MARSHES OF THE GULF AND ATLANTIC COASTS OF THE UNITED STATES

Judy P. Stout

INTRODUCTION

Salt marshes may be characterized on the basis of the frequency of tidal inundation into (a) regularly flooded - flooded by most high tides and (b) irregularly flooded - flooded infrequently in a pattern not related entirely to the local tidal regime (Uhler and Hotchkiss, 1968). Regularly flooded marshes are typically dominated by Spartina alterniflora (saltmarsh cordgrass) and have been extensively studied along the US Atlantic coast and Gulf of Mexico (see summaries by Day, Smith, Wagner and Wilmer, 1973; Cooper, 1974; Pomeroy and Wiegert, 1981). The black needlerush (Juncus roemerianus) is the dominant marsh plant of irregularly flooded marshes. Though considerable information has been developed concerning the structure and function of Gulf coast irregularly flooded marshes (Stout, 1984), little work beyond vegetational descriptions and primary productivity studies has been provided for Atlantic Juncus marshes (Marshall, 1974). Basic features of the two marsh types have been compared by de la Cruz (1980).

The black needlerush (Juncus roemerianus) occurs along the US Atlantic and Gulf of Mexico coasts between latitudes 25°N and 42°N, reaching its northern limit in New Jersey. Of the 3,174,333 hectares (ha) of marsh area in the eastern USA, 10.06 per cent (319,383 ha) is dominated by this species, 170,067 ha in the Gulf of Mexico and 149,316 ha along the Atlantic coast (Eleuterius, 1976). Juncus marshes most frequently occur along the shores of barrier island estuaries (North Carolina, Mississippi and Alabama), the upper reaches of river estuaries (Louisiana and South Carolina) or low-energy frontal shorelines (Florida west coast).

Physicochemical Environment

Irregularly flooded marshes are found on protected, flat to gently sloping coastlines with elevations generally above mean low water. Elevations from 1.64 to 3.24 feet (MLW) have been reported (Table 42.1). Tidal regimes vary from semi-diurnal (Atlantic coast) to mixed (Florida west coast) to diurnal (northern Gulf of Mexico) (NOAA, 1985). Tides are of low amplitude, usually less than 1.0 m. In general, irregularly flooded marshes are subjected to long

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Table 42.1: Juncus marsh elevation/tidal flooding

Location	Elevation	Tidal flooding	Reference
North Carolina	1.62 ft (MSL)	1.62 ft (MSL)	Waits (1967)
South Carolina		60 min/day	Stalter (1968)
NW Florida	3.24 ft (MLW)	81/yr	Kurz and Wagner (1957)
Mississippi:			
Short		5.8%/yr	Hackney and de la Cruz (1982)
Tall		12.0%/yr	Hackney and de la Cruz (1982)
	0.54-0.75m(MLW)		Eleuterius and Eleuterius (1979)
Gulf Coast	0.5-1.0m(MLW)		Stout (1984)

periods of exposure, especially during winter months of less frequent inundation.

High, flat coastal plains, small tidal ranges and barrier features combine to minimize the influence of regular lunar tides in these marshes. The extent and frequency of tidal flooding of Juncus-dominated marshes is consequently dependent upon wind speed and direction and other periodic, but non-cyclic events, such as hurricanes and storms. Flooding patterns vary considerably from marsh to marsh and even between years within a marsh system.

High precipitation rates (48 inches, Atlantic; 48-56 inches, Central Gulf) and subsequent freshwater discharge into Juncus-dominated marshes couple with infrequent tidal inundation to produce lower salinities than in regularly flooded, Spartina alterniflora marshes (Table 42.2). Juncus roemerianus dominates over a wide range of salinities from oligohaline (2.5-15.0 ppt) river mouths (Hackney and de la Cruz, 1978) to saline barrier sounds (21.6-32.4 ppt) (Stout, unpublished). Hypersaline conditions in many Texas coastal areas exclude Juncus.

The climate of Juncus-dominated US coastlines ranges from temperate (N. Atlantic) to near tropical (Florida). Marshes are replaced by mangrove swamps in south Florida due to the absence of killing winter frosts.

COMMUNITY STRUCTURE

Flora

Only descriptions of diatom and blue-green algal communities have been studied in Juncus marshes of the Gulf coast. Diatoms exhibit a continuous but heterogeneous benthic marsh cover both in areas

Table 42.2: Marsh interstitial soil water salinity

Location	Salinity (ppt)	Reference
North Carolina	1.75- 28.7	Foster (1968)
South Carolina	1.0 - 26.0	Stalter (1968)
NW Florida	13.2 - 19.1	Lindberg and Harris (1973)
Alabama	0.0 - 22.0 21.6 - 32.4	Ivester (1978) Stout (Unpublished)
Mississippi	0.0 - 9.0 2.5 - 15.8 15.5 ± 1.1	Bishop (1981) Hackney and de la Cruz (1978) Eleuterius and Caldwell (1981)
Louisiana	1.2 - 43.3	Penfound and Hathaway (1938)

with and without canopy vegetation. Sullivan (1978) identified 119 diatom taxa in Mississippi with significant differences between five canopy types (Spartina alterniflora, S. patens, Juncus roemerianus, Distichlis spicata and Scirpus olneyi) for diatom species diversity (H') and number of taxa in a sample(s). The most abundant diatom species was Navicula tripunctata, which accounted for 21.5 per cent of the individuals identified. The greatest number of species (89) was found under D. spicata and the lowest in Juncus. Only seven species were restricted to a single spermatophyte canopy. Sullivan (1978) suggested that salt marsh sediments do not constitute a stressful environment for the well-adapted diatom communities. The highly dynamic nature of the marsh and heterogeneity of benthic microniches prevent dominance of a community by a single taxon and explain the presence of restricted taxa.

One hundred of the Mississippi diatom taxa have also been reported in the marshes of Delaware and/or New Jersey (Sullivan, 1975, 1977, respectively), suggesting a single, basic edaphic diatom assemblage may be indigenous to Atlantic and Gulf coast salt marshes.

Comparison of edaphic diatoms and diatoms epiphytic on red algae associated with dead S. alterniflora revealed higher diversity in the edaphic community (31 epiphytic species, 43 edaphic species) (Sullivan, 1982). However, the two communities shared 63.2 per cent of the maximum similarity possible. Dominant taxa of both communities were Anaulus balticus, Fragilaria atomus, F. pinnata and Nitzchia minutula.

Experimental removal of a canopy of Distichlis spicata reduced diatom species diversity (H') and the number of taxa (Sullivan, 1981). High light intensity from canopy removal in conjunction with nitrogen enrichment increased the relative abundance of N.

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gandersheimensis, whereas natural canopy light intensity plus enrichment greatly stimulated N. perversa growth (Sullivan, 1981).

In contrast to diatoms, a single, nearly homogeneous community of blue-green algae has been described by Sage and Sullivan (1978), under the same five spermatophyte canopies in Mississippi. Twenty-five species of blue-green algae were identified. The community was dominated by three species: Schizothrix calcicola (40.5 per cent annual relative abundance), Anacystis montana (17.4 per cent annual relative abundance), and A. aeruginosa (16.4 per cent annual relative abundance). A high of 20 species was associated with Juncus and a low of 14 species was associated with S. patens. Twenty species were found in all habitats.

The composition of the spermatophyte community varies with the influence of freshwater input and consequent average salinities, lower estuarine mesohaline to polyhaline irregularly flooded marshes comprise a nearly homogeneous community of Juncus roemerianus with a fringe of intertidal short to medium Spartina alterniflora. Different height forms of Juncus may be seen along a transect from the shore to upland with shorter forms further inland (Stout, 1984). Other important species are Distichlis spicata in more saline areas of the marsh and S. patens in the upper marsh meadow. Hypersaline salt flats may be found in some Juncus marshes. These zones are sparsely vegetated with blue-green algae mats, Salicornia spp., Batis maritima and a fringe of D. spicata. Within the upper marsh meadow and other isolated elevated areas the salt shrubs Baccharis halimifolia and Iva frutescens may dominate (Stalter, 1968).

As freshwater impact lowers average salinities, the species diversity of the spermatophyte community increases and dominants consist of several species. Forty species of marsh plants were found by Hackney and de la Cruz (1982) in an oligohaline brackish Juncus marsh in Mississippi. Such oligohaline irregularly flooded 'mixed' communities have been described by Gabriel and de la Cruz (1974) in Mississippi and in North Carolina by Foster (1968) and Cooper and Waits (1973). Spartina alterniflora is of low dominance, but increasing importance of S. cynosuroides is seen in these more brackish settings. Salt flats are absent.

Fauna

Meiofauna were dominated by nematodes in irregularly flooded marshes of Alabama (Harp, 1980) and Mississippi (Humphrey, 1979). Harp (1980) identified ten major taxa under Juncus and S. alterniflora canopies. In S. alterniflora, nematodes contributed 62-77 per cent of the total meiofauna over a two-year period, harpacticoid copepods 25 per cent and oligochaetes 2 per cent. Abundance peaked in March, fell to a minimum in June, then increased through the fall and winter.

Meiofauna of Juncus habitats were also dominated by nematodes (52-57 per cent), with harpacticoid copepods comprising 26 per cent, oligochaetes 10 per cent, and polychaetes 3 per cent of the total number of individuals. The polychaete Manyunkia aestuarina was more numerous in Juncus than in Spartina, but did

not fluctuate in abundance as widely over the year in Juncus.

Dominant copepods were Microarthridion littoral (49.5 per cent) in Spartina, and Schizopera sp. (44.7 per cent) in Juncus (Harp, 1980). Of the 14 harpacticoid copepods identified, Harp (1980) found twelve under both canopies. Three species (Schizopera sp., Phyllopodopsyllus aegypticus and Robertsonia sp.) were restricted to Spartina canopies. Species diversities were not significantly different between canopy types.

In a brackish mixed marsh of St Louis Bay, Mississippi, Humphrey (1979) found meiofauna dispersed throughout the marsh with a high degree of similarity among canopy associations. Within stands of short and tall Juncus, S. patens, S. cynosuroides and Phragmites australis, eight major taxa were identified. Meiofauna were dominated by nematodes and foraminiferans.

Subrahmanyam, Kruczynski and Drake (1976) provide the only comprehensive picture of the macroinvertebrate community in saline Juncus marshes. Significant community changes were seen near the salt flat dividing the marsh into two distinct invertebrate species communities. They were characterized by Subrahmanyam et al. (1976) as a low marsh/upper marsh community dominated by Littorina irrorata, Cyathura polita, and tanaidaceans, with several abundant polychaetes (Scoloplos fragilis, Neanthes succinea and Laeonereis culveri). Mollusk populations increased toward the salt flat. A high marsh community existed with abundant fiddler crabs (Uca spp.) and the gastropods Melampus bidentatus and Cerithidea scalariformis.

Four major taxa comprised the invertebrate community, Mollusca (31 per cent), Annelida (24 per cent), insect larvae (1 per cent) and Crustacea (44 per cent). Nineteen species (39 per cent) were found in all four zones, whereas 11 species were found in only one zone. Unique species were typically estuarine forms found in the marsh only on flooding tides (e.g. Haminoea succinea, Taphromysis bowmani and Mysidopsis almyra). Sixteen species were designated abundant resident species, occurring in at least three seasons and with a mean density of greater than $3/m^2$ per season. Maximum late winter density ($578/m^2$) corresponded with recruitment of juveniles of the mollusks Littorina irrorata, Cyathura polita, Melampus bidentatus, Modiolus demissus (= Geukensia demissus) and Cyrenoidea floridana and the crustacean Sesarma reticulatum. Densities were lowest in summer ($375/m^2$) due to predation by fish.

No significant monthly density variations were detected, indicating fairly stable invertebrate populations (Subrahmanyam et al., 1976). However, low marsh zones had significantly more species than did the upper marsh. This may be caused by greater accessibility of the low marsh to estuarine organisms. Zonal differences were also seen in higher diversity in the low marsh than in the upper marsh. A second contributing factor to higher density and diversity within the low marsh may be the greater availability of organic detritus in this zone (Coults, 1969).

Mollusks and arthropods dominated an oligohaline Juncus marsh at Bay St Louis, Mississippi (Humphrey, 1979). Five stations were sampled based upon the species of vascular plant present: short and tall Juncus, Spartina cynosuroides, S. patens,

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and a mixed community of S. cynosuroides, S. alterniflora and Phragmites australis.

As in north Florida, the low marsh Juncus contained the greatest diversity and density of invertebrates. Soil pH, phosphorus content, and free soil water were positively correlated with abundance. Dominant species by both density and biomass were: low marsh Juncus - the bivalves Polymesoda caroliniana and Geukensia demissa, and the snail Neritina usnea (=Neritina reclinata) and high marsh Juncus - Melampus bidentatus, Uca sp., and Polymesoda caroliniana. Littorina irrorata were of minimal importance, found only infrequently in samples, perhaps because of the lower salinities ($x = 7.58$ ppt) compared to the north Florida marsh ($x = 15$ o/oo) (Humphrey, 1979).

In a third community study of macroinvertebrates, pure stands of Juncus roemerianus, intertidal Spartina alterniflora, and Distichlis spicata along a salt flat in Alabama were sampled by Ivester (1978) for macroinvertebrate community comparisons. A total of 18 species were identified along with unidentified oligochaetes, insects, and a capitellid polychaete. Oligochaetes dominated each of the three communities, ranging in relative abundance from 80 per cent in Spartina alterniflora to 53 per cent in Distichlis spicata. Six macroinvertebrate species comprised over 90 per cent of total numbers of the community in each zone, though species and relative abundance differed between zones. Littorina irrorata and Guekensia demissa were important only in Spartina stands. L. irrorata was replaced by Melampus bidentatus and increased numbers of Neritina reclinata in Juncus and Distichlis. Polymesoda caroliniana was the prevalent bivalve of the Juncus zone, as seen in both north Florida and Mississippi (Subrahmanyam et al., 1976; Humphrey, 1979). There was no abundant bivalve found near the Mississippi salt flat (Humphrey, 1979).

The insect populations of a Mississippi Juncus-dominated marsh were assessed by Parsons (1978). A total of 265 species representing 72 families and nine orders were collected using standard sweepnet techniques. Only four Diptera, one Hymenoptera, and one Hemiptera occurred consistently throughout the year. Numerically, the dipterans and hymenopterans were codominants throughout the year and were joined during the warmer months by the equally abundant homopterans.

Fish communities are dominated by physiologically euryhaline and holeyhaline fish (Kilby, 1955; Subrahmanyam and Drake, 1975; Subrahmanyam and Coulas, 1980; Hackney and de la Cruz, 1981a). Of 49 species collected in a Florida Juncus marsh by Kilby (1955), over two-thirds were predominantly freshwater to brackish water species. These species comprised approximately 87.7 per cent of the total number of individuals collected. An oligohaline (0.5-5.0 ppt) marsh in Mississippi was distinctive in that freshwater centrarchids (Micropterus salmoides and Lepomis macrochirus) were major predator species (Hackney and de la Cruz, 1981a).

Permanent residents are dominated by cyprinodont species. Subrahmanyam and Drake (1975) attributed 53-90 per cent of total monthly biomass to adults of Fundulus similis, F. grandis and Cyprinodon variegatus. Less common were Adinida xenica, Poecilia

latipinna, Lucania parva and F. confluentus. Most resident species have protracted or continuous spawning seasons as evidenced by the year-round presence of juveniles and by species life history studies. Additional species, including Mugil cephalus, Anchoa mitchilli, Membras martinica and Brevoortia patronus were persistent in an oligohaline marsh creek in Mississippi and contributed up to 99.9 per cent of total catches in spring and winter (Hackney, 1977). Marsh resident species are typically opportunistic omnivores, capable of utilizing different food depending on availability.

Leiostomus xanthurus juveniles were common in spring and late fall, accounting for 16-90 per cent of catch by numbers and biomass (Subrahmanyam and Drake, 1975). Adults were caught in high tide samples in summer and fall. Juvenile mojarras (Eucinostomus argenteus) occurred primarily in fall, comprising 14-72 per cent of the catch by numbers (Subrahmanyam and Drake, 1975). Anchoa mitchilli was represented in most catches by juveniles only between March and September. Two other nursery utilizers, Mugil cephalus and Lagodon rhomboides, were seasonally abundant (Subrahmanyam and Drake, 1975). Most juveniles of these two species and Leiostomus xanthurus leave the marsh creeks by June (Zilberberg, 1966).

Foraging species are captured only on high tides as they make use of increased feeding habitat during tidal flooding of the marsh surface. Most foragers are estuarine residents and their numbers and diversity depend upon the proximity of the marsh to estuarine or nearshore waters. Eight species were categorized by Subrahmanyam and Drake (1975) as foragers. Dominants included Hyporhamphus unifasciatus, Bairdiella chrysura and Cynoscion arenarius.

Species categorized as sporadic visitors include Polydactylus octonemus (Subrahmanyam and Drake, 1975), Anguilla rostrata, Archosargus probatocephalus, Cynoscion nebulosus, Arius felis, and Sphyraena barracuda (Kilby, 1955; Hackney and de la Cruz, 1981a).

ENERGY DYNAMICS

Primary productivity

Primary production of aerial biomass in Juncus marshes varies with geographic location, height form and method of estimation (Table 42.3). Values range from 243 g m⁻² in a Florida high marsh (Kruczynski, Subrahmanyam and Drake, 1978a) to 3,078 g m⁻² in an Alabama marsh (Stout, 1978)(Table 42.3). Only Kruczynski et al., (1978a) provided data on different height forms of Juncus and demonstrated a significant decline in production landward, parallel with decreasing mean height and leaf diameter.

Production of new tissue occurs year-round in Juncus roemerianus. Gulf coast studies indicate significant seasonal fluctuations in standing crop production and in the ratio of live/dead tissue (de la Cruz, 1974; Hackney et al., 1978; Stout, 1978). Peak production occurs in spring and early summer. Dead biomass increases through the fall to highs in the winter, during periods of infrequent inundation. In contrast, Atlantic coast marshes

Table 42.3: Aboveground primary production of *Juncus roemerianus*

Location	g/m ² /yr	Method	Reference
North Carolina	1,361	Changes in living and dead standing crop	Waits (1967)
	735	Model	Williams and Murdoch (1968)
	2,627	Peak standing crop	Williams and Murdoch (1972)
	560	Growth/death	Foster (1968)
Georgia	2,200	Wiepert and Evans (1964)	Gallagher <u>et al.</u> (1980)
		Wiepert and Evans (1964)	Kruczynski <u>et al.</u> (1978a)
Florida: Low Marsh	949	Peak standing crop	Heald (1971)
	595	Peak standing crop	Stout (1978)
	243	Mean monthly standing crop	
High Marsh	849	Smalley (1959)	
		Milner and Hughes (1968)	
Alabama	1,745	Max.-min. Model	Hackney <u>et al.</u> (1978)
	1,449	Max.-min. Model	
	3,078	Max.-min. Model	
	1,180	Max.-min. Model	
	580	Max.-min. Model	
Mississippi	1,697	Smalley (1959)	de la Cruz (1974)
	1,700	Max.-min. Model	de la Cruz and Hackney (1977)
Louisiana	2,797	Average of methods	Gosselink <u>et al.</u> (1977)

exhibit only slight seasonal changes in standing crop and no seasonal changes in live/dead ratios (Waits, 1967; Williams and Murdoch, 1972; Gallagher, Reimold, Linthurst and Pfeiffer, 1980).

Belowground production greatly exceeds aboveground production and ranges from $4,425 \text{ g m}^{-2}$ to $5,074 \text{ g m}^{-2}$ for standing crop estimates in the upper 20 cm of the soil (Table 42.4). Stout (1978), de la Cruz and Hackney (1977) and Gallagher (1974) found declining standing crop with depth in the sediments. The bulk (up to 80 per cent) of the root/rhizome material is in the upper 10-15 cm. This large pool of biomass may provide valuable energy if it finds its way into the food web and further assessment of its role is important.

Detrital Production and Decomposition

Irregular tidal inundation and long periods of exposure result in large quantities of standing dead biomass and debris (detritus) on the marsh surface. As much as $1,180 \text{ g m}^{-2}$ of Juncus debris was collected by Hackney and de la Cruz (1981b) on the marsh floor. Sporadic tidal transport of material combined with low decomposition rates contribute to this build-up.

Juncus roemerianus decomposes at a slower rate than has been reported for Spartina alterniflora due to a combination of factors, including high fiber content in Juncus tissues and environmental conditions not conducive to maximum decomposer activities. Annual loss of aboveground dead tissue to decomposition of Juncus ranges from 38 per cent (Heald, 1971) in Florida mangrove associations to 65 per cent in a north Florida Juncus marsh (Kruczynski et al., 1978b) (Table 42.5). Average rates appear to be approximately 47 per cent loss yr^{-1} . Decomposition of below-ground tissues is much slower because of anaerobic conditions in the substrate (Table 42.5). Maximum loss from limited studies is 25 per cent (Stout and de la Cruz, 1978).

Following decomposition, Juncus roemerianus detritus has notably higher total amino acids, crude protein and amino acid/crude protein ratios (de la Cruz and Poe, 1975).

Utilization and Transport of Organic Material

Parsons and de la Cruz (1980) found that three species of conocephaline grasshoppers were major insect herbivores grazing on the leaves of Juncus. They ingested 104.6 kJ m^{-2} of the distal portions of the leaves or about 0.03 per cent of net primary production. Other major consumers may be large mammals such as nutria and muskrat, though data are not available.

Hackney and Haines (1980) compared $^{13}\text{C}/^{12}\text{C}$ ratios in the tissues of marsh fauna to determine possible food sources. Marsh faunal ratios exhibited no significant differences attributable to type of dominant plant but appeared to reflect a significant input of allochthonous terrestrial material by river flooding.

Hackney and de la Cruz (1979) found that the same Mississippi study marsh imported a net of $168\text{g m}^{-2}\text{yr}^{-1}$ of particulate matter, 16 per cent of which was organic carbon. Marsh bivalves such as Polymesoda caroliniana can remove up to 3.4 mg

Table 42.4: Belowground primary production of Juncus roemerianus

Location	g/m ² /yr	Method	Reference
Georgia	5,074 (20 cm deep)	Standing crop	Gallagher (1974)
Florida: Low Marsh	4,573	Mean monthly standing crop	Kruczynski et al. (1978a)
Upper Marsh	4,063		
High Marsh	5,140		
Alabama	6,340	Peak standing crop	Stout (1978)
	4,425	Mean monthly standing crop	
	7,578	Smallley (1959)	
	5,212	Milner and Hughes (1968)	
Mississippi	1,360	Max.-min. Model	de la Cruz and Hackney (1977)

Table 42.5: Annual decomposition rates (as percentage of total loss) of Juncus roemerianus

State	Mesh size (mm)	Aboveground		Reference
		loss/year (%)	Belowground loss/year (%)	
MS	5.0	40		de la Cruz and Gabriel (1974)
MS	3.0	48	5 cm = 17.5 15 cm = 7.9	Hackney and de la Cruz (1980)
FL	5.0	65		Kruczynski <u>et al.</u> (1978b)
	2.5	38		Heald (1971)
AL	1.25	44	10 cm = 25 20 cm = 22	Stout and de la Cruz (1978)

day⁻¹ of this organic material (Kraeuter, 1976). The marsh exported 310 g m⁻² yr⁻¹ of debris (large pieces of dead plants) and 0.5 kg yr⁻¹ of living biomass (Hackney, 1977).

Non-periodic events such as storms and hurricanes may play a significant role in the coupling of Juncus marsh energy production with estuarine food webs. A single low-level hurricane removed approximately 226 x 10³ kg of unattached dead material, from a Mississippi Juncus marsh, and redeposited as wrack 7.7 x 10³ kg. Net result was a removal of 227 g m⁻² of dead material from the entire marsh (Hackney and Bishop, 1981).

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Chapter Forty-three

A COMPARISON OF VASCULAR PLANT COMMUNITIES IN TIDAL FRESHWATER AND SALTWATER MARSHES

William E. Odum and John K. Hoover

INTRODUCTION

Tidal freshwater marshes and salt marshes provide an interesting opportunity to compare the effects of a single source of stress, salinity, on the structure of wetland plant communities. In other respects, such as geographical location and range of tidal fluctuation, these two types of wetlands are often very similar.

Tidal freshwater marshes typically lie at the head of an estuary nearest the source of freshwater input. By definition they have a mean annual salinity of less than 0.5 ppt and concentrations of sulfur three orders of magnitude lower than seawater. Occasionally, they may experience salinities as high as several ppt during droughts and periods of low freshwater flow. Tidal fluctuations are comparable to other locations further down the estuary. Odum, Smith, Hoover and McIvor (1984) have reviewed the available literature on this type of wetland.

Salt marshes lie further down the estuary and are subject to mean annual salinities greater than 15-18 ppt. These higher salinities pose a significant source of stress to most vascular plant species. Frey and Basan (1978), Teal (1986), and Nixon (1982) provided reviews on salt marshes.

The Objective of this Chapter

In this review apparent differences in vascular plant community structure between these two types of wetlands are compared. Ideas about these differences come from the authors' own observations and research and from published literature. In each case it is hypothesized that the difference originates from the relative lack of salinity stress in tidal freshwater marshes and the resultant response of the plant community as affected by interspecific competition and local physical conditions (i.e. sediment type, marsh geomorphological developmental stage, climate, etc.).

HYPOTHETICAL DIFFERENCES

Plant Species Diversities and Dominance

In the regularly flooded portion of salt marshes, the vascular plant

species diversity is usually low. There are rarely more than 15 species which grow intertidally and 30 or 40 species in the entire portion of the marsh which is inundated monthly. Typically one species, such as *Spartina alterniflora*, dominates the intertidal or low marsh, whereas three or four species dominate the irregularly flooded high marsh (Miller and Egler, 1950; Zedler, 1977; Pemadasa, Balasurbramaniam, Wijewansa and Amarasinghe, 1979).

In marked contrast, tidal freshwater marshes on the east coast of the United States usually have 25-40 species growing intertidally and 60 to 100 species in sections of the marsh which are flooded frequently (Odum et al., 1984). Moreover, single species rarely dominate the marsh throughout the year as occurs in salt marshes. It is not unusual to have combinations of 12 or more dominant species of annual and perennial emergent macrophytes more typical of non-tidal wetlands than of saline wetlands (Simpson, Good, Leck and Whigham, 1983).

These differences in species diversity and dominance, while easily demonstrated with the simplest sampling technique, are also obvious to even the most casual observer, particularly during the height of the growing season. The salt marsh looks relatively simple floristically while the tidal freshwater marsh looks complex.

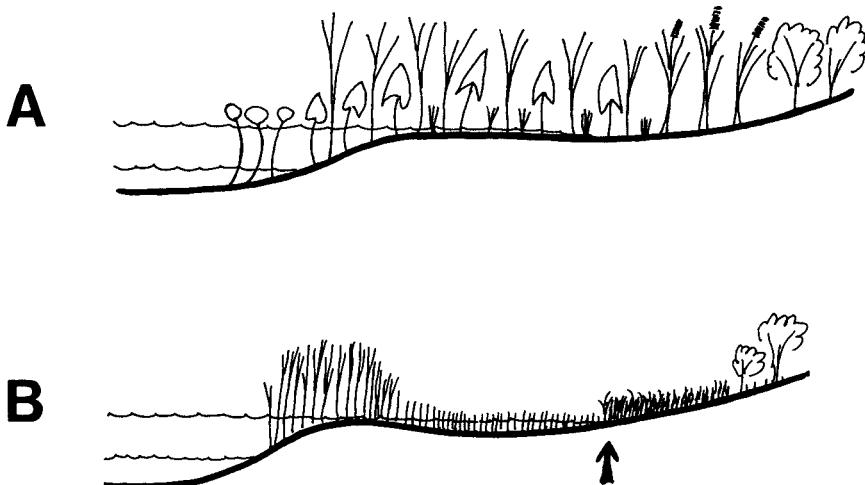
Zonation

Salt marshes usually exhibit distinct zonation (Nixon and Oviatt, 1973) (Figure 43.1). The low marsh is separated from the high marsh at approximately the mean high tide mark. Habitat overlap is minimal between zones because species are restricted in their distribution, e.g. *Spartina alterniflora* occurs almost exclusively in the low marsh and *Spartina patens* in the high marsh (Miller and Egler, 1950). Zonation is probably a result of the interplay between salt water, soil pore water movement and evaporation, regular inundation and interspecific competition mediated by differences in physiological tolerance of the plants.

In tidal freshwater marshes, distinct zonation is usually absent (Figure 43.1). This is because domination of specific intertidal zones by a single species is rare. Although patterns of dominance occur, most species are found in most habitats (Whigham, McCormick, Good and Simpson, 1978) because many produce seeds which are widely dispersed. In the mid-Atlantic states, plants such as wild rice, *Zizania aquatica*, and arrow-arum, *Peltandra virginica*, may dominate at many points along the marsh elevational gradient. Although there are often major differences in species composition at the ends of the elevational gradient, transition of species combinations along the gradient is gradual and relatively indistinct. One of the few exceptions to this tendency of indistinct zonation occurs on very gradual marsh gradients where spatterdock, *Nuphar luteum*, may form a band at the lowest elevation and the cattail, *Typha latifolia*, or the common reed, *Phragmites australis*, exists in a dense stand in the higher part of the marsh.

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Figure 43.1: A comparison of patterns of zonation in (A) tidal freshwater marshes and (B) salt marshes. Note the increased standing crop of Spartina alterniflora found along the stream banks of many salt marshes and the sharp delineation between the low and high marshes (arrow)



Tree/Marsh Delineation

In saline environments at tropical latitudes, mangrove trees successfully colonize most of the intertidal zone (see Odum, McIvor and Smith, 1982, for a review of mangrove zonation and colonization). For example, the red mangrove, Rhizophora mangle, occurs at and below the mean low tide mark in south Florida. At latitudes higher than 30°N, however, the combination of salt stress and freezing temperatures effectively excludes trees from the saline intertidal zone.

Trees occur in tidal freshwater wetlands at least as far north as latitude 45°N (central New England), but usually in the higher portion of the intertidal zone. Tidal freshwater swamps are common in the central and south Atlantic states where species such as bald cypress, Taxodium distichum, and gums, Nyssa sylvatica var. biflora and N. aquatica, occur intertidally.

Exceptionally little research has addressed the question of the demarcation between marsh (dominated by emergent grasses, sedges and shrubs) and swamp (dominated by trees) in tidal freshwater environments. In other words, why do tidal swamps exist in one location and tidal marshes in a similar, nearby site? In a preliminary fashion, we hypothesize that the distribution of tidal freshwater swamps is controlled by a combination of (1) flooding depth (most trees need a period of little or no flooding to become

established), (2) presence or absence of dissolved salts in the water, (3) local conditions of land subsidence and sea level rise. For example, a tidal cypress/gum swamp might exist at a site which (1) was formerly above mean high tide and flooded only very occasionally so that seedlings could become established, (2) subsequently was moved into the intertidal zone by sea level rise or local subsidence, and (3) was not subject to local incursions of salt water. Many variations might exist. If conditions (1) and (2) occurred, but salt water intruded during drought, then the swamp tree species might be limited to the highest portion of the tidal freshwater wetland where they would be least likely to be subjected to long-term saltwater stress.

In summary, we have suggested the following about tree/marsh zonation in tidal salt water and tidal freshwater.

- (1) The topic is little studied, particularly in tidal freshwater.
- (2) Trees occur in tidal freshwater much further north than in salt water.
- (3) The factors controlling intertidal distribution of trees in tidal freshwater need to be investigated.

Macrophyte Distribution in the Lower Intertidal

In salt marshes, vascular plants are typically found only in the upper two-thirds of the intertidal zone (Redfield, 1972), while the lower third is devoid of emergent marsh plants and consists of bare soil and, occasionally, layers of algae (Figure 43.2). This lack of colonization is probably a result of the combined stress of salt water and duration of flooding. Exceptions to this pattern do occur in regions such as the northern coast of the Gulf of Mexico where the tidal range is very slight and Spartina alterniflora extends its range completely to the low tide mark (Eleuterius, 1984).

Hoover's (1984) research in Virginia suggests that tidal freshwater plants are able to colonize all of the intertidal zone if slope, exposure and sediment characteristics are suitable (Figure 43.2). We hypothesize that the complete colonization of the intertidal zone in tidal freshwater is due to minimal salt stress and the resulting larger pool of emergent and floating-leaved vascular plants which can grow there.

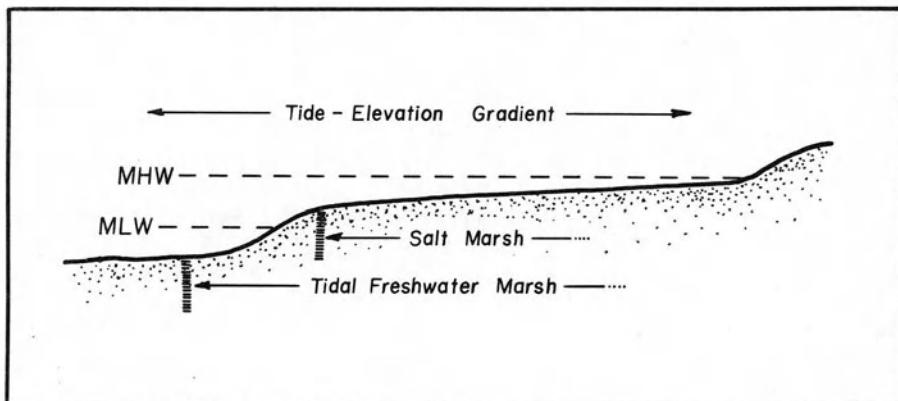
Seasonal Succession of Dominant Macrophytes

Salt marshes generally have the same dominant species throughout the growing season (Nixon and Oviatt, 1973). These dominants are usually perennial graminoids with extensive underground rhizome systems (such as species of Spartina).

In sharp contrast (Figure 43.3), tidal freshwater marshes, at least on the east coast of North America, exhibit pronounced seasonal change in dominant vegetation (Whigham et al., 1978). Perennials such as Peltandra virginica and Acorus calamus reach peak biomass in late June to early July in Virginia and then give way to annuals such as Zizania aquatica and Impatiens capensis.

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Figure 43.2: Extent of colonization of the intertidal zone in salt marshes and tidal freshwater marshes. This is also depicted in Figure 43.1. Tidal ranges are assumed to be greater than 1 m



which reach peak biomass in late August (Odum et al., 1984). A third dominance peak may occur in mid-September when annuals such as Polygonum arifolium and Bidens laevis become dominant in terms of biomass (Whigham et al., 1978).

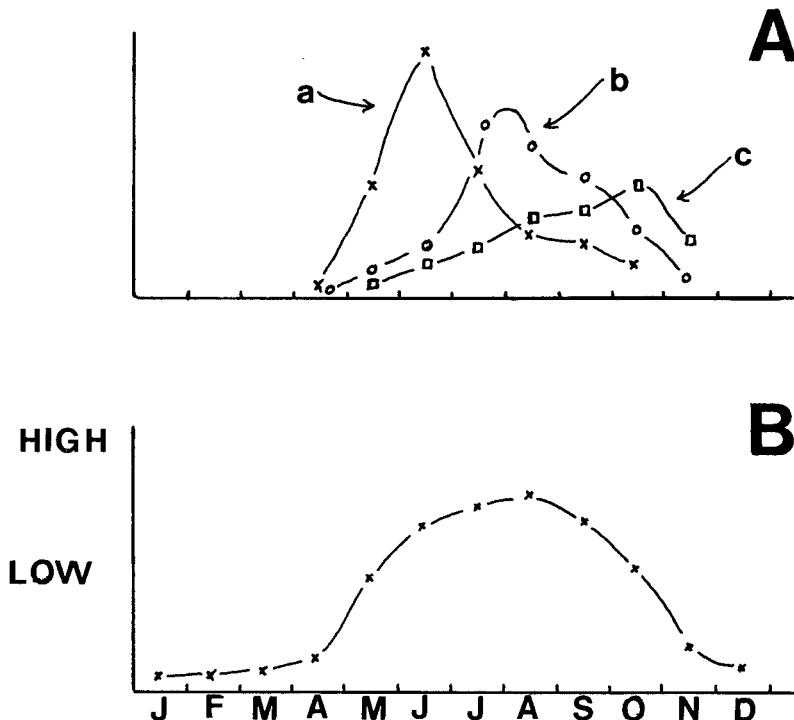
Presumably, this complex seasonal succession in tidal freshwater can be traced to (1) minimal salt stress and (2) the resultant large species pool which is present. Early in the growing season, the perennials, with supplies of energy stored in their rhizome systems, grow luxuriantly. During the hotter months of the summer, more heat-tolerant plants, mostly annuals, become dominant. The result is a complicated sequence of at least two or three 'waves' of plant species dominance between spring and autumn.

Patterns of Primary Production

The horizontal distribution of vascular plant primary production in salt marshes (Figure 43.4) has a typical pattern of high production (and standing crop) along the creek bank and levee, and lower amounts of production in the middle sections of the marsh (the short S. alterniflora zone) up to high tide (summarized in Pomeroy and Wiegert, 1981). Production in the high salt marsh may be low or comparable to the streambank marsh (Nixon, 1982). Reduced production in the mid-sections of the marsh and variable production in the high marsh are due to the interplay of a variety of factors, including reduced tidal flushing, high evaporation rates, and resulting elevated concentrations of salts and sulfides in the pore water of the sediments.

Little published data exist concerning the horizontal distribution of vascular plant primary production in tidal freshwater marshes. Our preliminary standing crop data suggest a more even

Figure 43.3: A comparison of temporal patterns of above-ground standing crops in (A) tidal freshwater marshes and (B) salt marshes. The tidal freshwater curves are composed of (a) broad-leaved perennials, (b) first group of annuals (with some perennial grasses), and (c) second group of annuals. See text for species examples



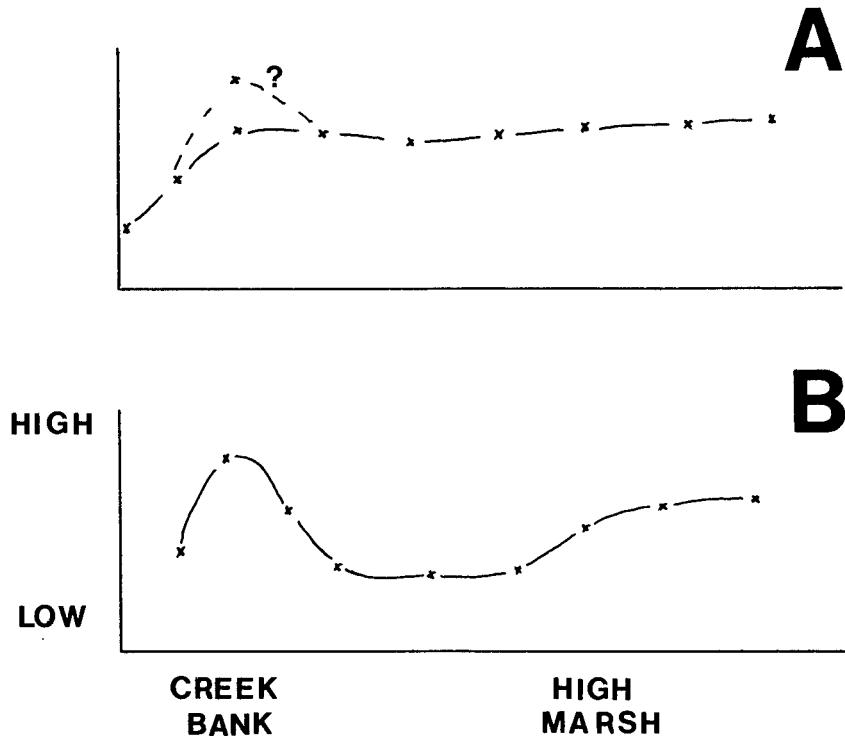
pattern (Figure 43.4) than in salt marshes. We have found a slightly elevated standing crop along creek banks and depressions, but a much more uniform distribution across the marsh surface to the rear of the marsh where a second minimal peak may occur if significant terrestrial drainage is present (i.e. a steep upland slope). We hypothesize that this uniform pattern results from the relatively dilute concentrations of salts and sulfides in interstitial pore water in tidal freshwater.

Total Primary Production

Estimates of annual primary production in salt marshes and tidal freshwater marshes at specific micro-locations have proven to be highly variable, but comparable. In other words, variation within

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Figure 43.4: Hypothetical comparison of annual primary production on a horizontal scale in (A) tidal freshwater marshes and (B) salt marshes. In certain locations, streambank productivity may be enhanced in tidal freshwater marshes



marshes is as great as variation between marshes. We suggest, however, that total system production may be significantly higher in tidal freshwater marshes. We base this suggestion upon the observation in the previous section of uniform, high primary production across the entire marsh in tidal freshwater. If this is true, then maximal sites within the marsh may be comparable in both systems, but the overall production integrated across the entire gradient in tidal freshwater marshes should be significantly greater. This idea needs to be tested at a variety of sites.

CONCLUSIONS

We have presented a hypothetical comparison of the structure of vascular plant communities in salt marshes and tidal freshwater

marshes. We have suggested that the presence of high concentrations of salts and sulfides in salt marsh water and low concentrations in tidal freshwater have led to significant differences in species diversity, dominance, zonation, tree/marsh delineation, distribution in the lower intertidal zone, seasonal patterns of succession, horizontal patterns of primary production and total system primary production.

The general lack of salt and sulfide stress in tidal freshwater marsh soils relative to salt marshes apparently leads to the following characteristics of the vascular plant community: (1) higher species diversity, (2) co-dominance by multiple species, (3) less distinct zonation, (4) colonization of coastal wetlands by trees (formation of swamps) much further north than in salt water, (5) colonization of the lower portion of the intertidal zone, (6) pronounced seasonal succession, (7) even, high primary production completely across the marsh elevational gradient and, perhaps, (8) higher total system primary production.

Obviously, these ideas must be tested more thoroughly. In addition, they can be criticized in at least two ways. First, all our examples come from the temperate east coast of the United States. These suggested tendencies may not be universal. Second, there are other possible explanations for our observations in combination or addition to water salinity. For example, higher species diversity in tidal freshwater might result at least partly from its closer proximity to seed sources in non-tidal freshwater marshes.

In conclusion, fundamental differences appear to exist between plant communities in tidal freshwater and salt marshes in response to contrasting concentrations of dissolved salts and, possibly, other factors. Clearly, more extensive research is needed to test these hypotheses.

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Chapter Forty-four

HERBIVORE POPULATION DYNAMICS IN INTERTIDAL MARSHLANDS: THE ROLE OF HOST PLANT NUTRITION

Robert F. Denno

INTRODUCTION

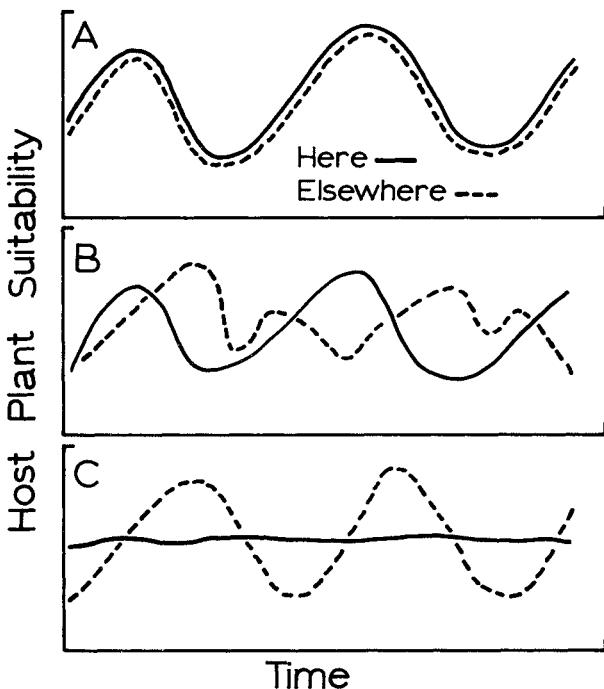
Several researchers in population dynamics have attempted to predict when insects will migrate based on changes in habitat quality. Several very general models have been proposed (Southwood, 1962, 1977; Solbreck, 1978; Denno and Grissell, 1979). Solbreck's (1978) model discusses an environment containing an archipelago of habitat patches variable in time and space and an insect which may respond with either immediate reproduction, migration, or diapause (Figure 44.1). For an insect to develop the appropriate strategy, it needs information concerning environmental variability in both spatial and temporal dimensions. Consequently, information is needed about the future quality of the immediate resource here, as well as the future quality of alternative patches elsewhere. Selection will make the appropriate life history decision.

For example (Figure 44.1A), if changes in the quality of resource patches here and elsewhere mimic each other, then diapause rather than migration should be favored when resources are unsuitable. Why move if you can't improve your situation? However, if changes in resource abundance (quality) here and elsewhere are not in phase, migration should be adaptive because as conditions deteriorate here they are improving elsewhere (Figure 44.1B). Also, migration should be favored if conditions are always suitable here, but oscillate between better and worse elsewhere. The opportunity to colonize a seasonally proliferating resource describes this situation (Figure 44.1C). These models are generally logical, but if we are ever able to predict the conditions that lead to migration, we must know the specific components of habitat favorability as they vary within and between habitats.

This chapter focuses on temporal and spatial variation in several habitat factors, particularly host plant nutrition, and its contribution to the population dynamics and migration behavior of a single herbivorous insect. The herbivore is a planthopper (Prokelisia marginata, Homoptera: Delphacidae) that inhabits the intertidal marshes of the Atlantic and Gulf Coasts where it occurs on its only host plant, the grass, Spartina alterniflora. My objectives include (1) demonstrating differences in the distribution and abundance of this planthopper in its various Spartina habitats and (2) trying to understand how factors like host plant quality con-

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Figure 44.1: Predicted life-history responses of herbivorous insects to spatial and temporal changes in the favorability of resources in patches here (—) and elsewhere (---). (A) Where changes in the favorability of patches here and elsewhere are similar, better alternatives are not available, and diapause rather than migration should be favored when the quality of all patches is low. (B) In contrast, if the favorability of patches elsewhere improves while the current patch deteriorates, migration should be favored. (C) If resources are permanently available in one habitat here yet fluctuate seasonally elsewhere, migrations to and from the temporary habitat can occur.



Source: From Solbreck (1978)

tribute to the performance, population dynamics, and migration behavior of Prokelisia.

STUDY ORGANISMS

Prokelisia marginata is the most abundant herbivore in Atlantic marshes where it feeds in the phloem cells of its host grass,

Spartina alterniflora (Denno and Grissell, 1979; Denno, Douglass and Jacobs, 1986). Using saw-like ovipositors, females insert their eggs between the ridges on the upper blade-surfaces of the grass. Eggs hatch and nymphs feed on the leaf blades passing through five instars or stages. In the mid-Atlantic states of the USA, there are three generations a year and nymphs overwinter by nestling into the thatch of the grass (Denno and Grissel, 1979; Tallamy and Denno, 1979).

Like most planthoppers, populations of Prokelisia are composed of two discrete wing-forms, thus facilitating the study of migration (Denno, 1976). There are macropterous individuals with fully developed wings, and brachypterous individuals with reduced wings that cannot fly. Macropters are capable of long distance flight and consequently are able to escape from unfavorable host plants and colonize new ones (Denno, 1983). Because of their flightlessness, brachypters can move only short distances up to several meters and are unable to track large-scale changes in the abundance and quality of their hosts (Denno, Raupp, Tallamy and Reichelderfer, 1980). However, brachypters have a reproductive advantage because they reproduce earlier and lay more eggs (Denno and McCloud, in press). Thus, as long as conditions remain favorable, brachypters have an advantage.

For planthoppers in general, wing-form is not inherited by any simple genetic rule and is polygenic in the few species studied (Kisimoto, 1956, 1965; Raatikainen, 1967; Roff, in press). However, there is a strong environmental component to wing-form determination. Individuals have the capability of molting into either a brachypter or a macropter. Various environmental cues trigger a developmental switch that determines wing-form. Crowding, host plant nutrition and temperature are three cues that influence wing-form in Prokelisia (Denno, Douglass and Jacobs, 1985).

The host plant of Prokelisia, Spartina alterniflora dominates the vegetation of many Atlantic coast marshes in North America where it grows predominantly below MHW level often in large pure stands (Denno, 1983). On Atlantic Coast marshes Spartina alterniflora occurs as two dynamically different growth forms in two fairly discrete habitats (Denno and Grissell, 1979). Along the depressed borders of tidal creeks and on bay edges, tall-form plants grow. Here, plants may reach 2 m in height. On the high flat marsh near MHW level, short-form grows where plants reach only 10-40 cm in height.

Short-form plants sprout in spring, die in fall, but remain standing through winter and have associated with them a thatch where nymphs overwinter. By contrast, tall-form plants obtain very large biomass in early summer, die back in fall, but due to the action of winds, waves, and ice are knocked over and finally sheared off completely during winter leaving exposed creek banks unsuitable as overwintering sites for Prokelisia. Thus, the Spartina system consists of two major habitat types, short-form grass on the high marsh that is persistent year round, and tall-form grass that is temporarily available during summer and fall for exploitation by planthoppers.

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PLANTHOPPER POPULATION DYNAMICS

Nymphs of Prokelisia overwinter on the high marsh and begin molting to adults in spring (Figure 44.2A). Because of the low elevation of the streamside habitat, short plants are often inundated during early spring. As a consequence, the offspring of first generation adults develop mostly on the high marsh. It is not until early summer (Figure 44.2B) that streamside Spartina grows tall enough for exploitation by planthoppers. During late spring and early summer, macropters migrate from the high marsh and colonize streamside vegetation where they oviposit. Some adults (both macropters and brachypters) remain on the high marsh and reproduce. During summer (Figure 44.2C), eggs hatch on streamside vegetation where huge populations of developing nymphs can occur. Much smaller populations of nymphs occur on the high marsh during summer. During fall (Figure 44.2D), nymphs on streamside vegetation molt mostly as macropters that migrate, colonize high marsh vegetation, and oviposit along with resident adults. These eggs hatch into the overwintering generation of nymphs and the cycle begins again (see Denno and McCloud, 1985 for details).

RESULTS AND DISCUSSION

In the sections that follow, I focus on an investigation of what factors are responsible for driving the population dynamics of Prokelisia. To do so I have divided the remainder of this report into three parts. First I investigate in the laboratory how two factors, host plant nutrition and crowding, affect the fitness of Prokelisia. Second, I review how these two factors influence the production of migrants. Last, I extend my laboratory findings to the field to explain the underlying mechanisms involved in the interhabitat migrations of Prokelisia as well as the consequences of these movements.

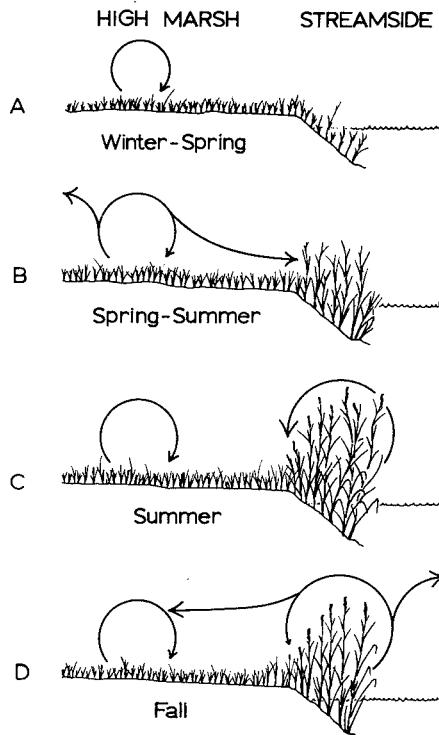
Planthopper Performance

The effects of host plant nutrition and crowding on the fitness of Prokelisia were examined by setting up a 2×5 factorial experiment in the greenhouse. By fertilizing some Spartina seedlings heavily and others lightly I was able to establish two nutritional categories of hosts that represent the extremes available in the field. On average, heavily fertilized plants contained 65 mg/g soluble protein, whereas lightly fertilized plants contained only 15 mg/g.

Five densities of newly hatched first instar nymphs were caged on the two nutritional categories of plants. The five densities were 1, 5, 10, 25 and 50 nymphs/tube cage. To correct for differences in plant size, these densities were ultimately expressed as load values (no. of nymphs/g of Spartina). Nymphs were allowed to feed, and the size of eclosing adults and their development time were measured.

Nymphal crowding had a profound effect on the development time to adult. Increasing the level of crowding from 2 to 75

Figure 44.2: Population dynamics and interhabitat migration in *Prokelisia marginata*. (A) Nymphs overwinter on the high marsh and begin eclosing to adults in spring. Because of the low elevation of the streamside habitat, plants remain inundated during early spring. As a consequence, the offspring of first-generation adults develop mostly on the high marsh. (B) It is not until early summer that streamside *Spartina* grows tall enough for exploitation by plant-hoppers. During late spring and early summer, macropters migrate from the high marsh and colonize streamside vegetation, where they oviposit. Some adults (both macropters and brachypters) remain on the high marsh and reproduce. (C) During summer, eggs hatch on streamside vegetation, where huge populations of developing nymphs occur. Smaller populations of developing nymphs occur on the high marsh. (D) Nymphs on streamside vegetation eclose mostly as macropters in fall; these macropters migrate, colonize high-marsh vegetation, and oviposit along with resident adults. These eggs hatch into the overwintering generation of nymphs. (See Denno and Grissell, 1979 for greater detail).



Source: From Denno and McCloud (1985)

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nymphs/g Spartina extended development time by more than ten days. The effect was general on all sexes and wing-forms (Denno et al., 1986). Interestingly, there was no effect of host plant nutrition on development time for any of the sexes and wing-forms (Denno et al., 1986).

However, host plant nutrition had a major effect on the body size of Prokelisia. The body length of both sexes increased when they were raised on nutritionally superior hosts compared to less nutritious ones, but females showed a proportionally greater increase. When raised on more nutritious seedlings of Spartina, the body length of females increased 7 per cent. We may ask what the fitness ramifications of large body size are. For Prokelisia, there is a significant positive relationship between average daily fecundity and body length (Denno and McCloud, 1985). Using this relationship and the body size data from the greenhouse experiment, a 25 per cent increase in daily fecundity should be realized by females feeding on the more nutritious grass (Denno and McCloud, 1985).

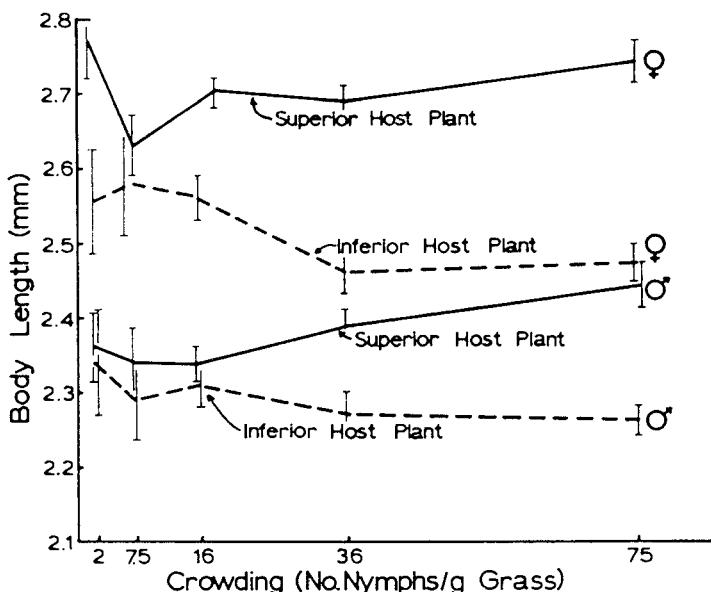
Perhaps the most interesting effect of the treatments on the body length of Prokelisia was a significant interaction between crowding and host plant nutrition (Denno et al., 1986). Crowding had a greater reducing effect on body length if hoppers were raised on marginal quality seedlings compared to nutritiously superior ones (Figure 44.3). Note that the body size decreases with crowding (= load) on inferior hosts (dashed lines) while it remains the same or increases slightly on superior hosts (solid lines). We can conclude that body size-mediated fecundity in Prokelisia is increased by feeding on nutritious host plants, that crowding reduces fitness by extending development time, and that superior host nutrition in part moderates the negative effects of crowding.

Production of Migratory Forms

To look at the effect of crowding and host nutrition on wing-form, I return to the results of the greenhouse experiment where five densities of nymphs were raised on both heavily and lightly fertilized seedlings of Spartina (see Denno and McCloud, 1985). The wing-form responses of males and females to crowding and host quality are different. On lightly fertilized grass (Figure 44.4A) proportionally more females molt to macropters as density increases. This is not the case with males where macroptery is high at low densities as well. At very low densities perhaps macroptery is favored in males to facilitate locating females by flight. On heavily fertilized hosts (Figure 44.4B) macroptery is suppressed at high densities for both males and females. However, at low densities males remain long-winged despite high host nutritional quality.

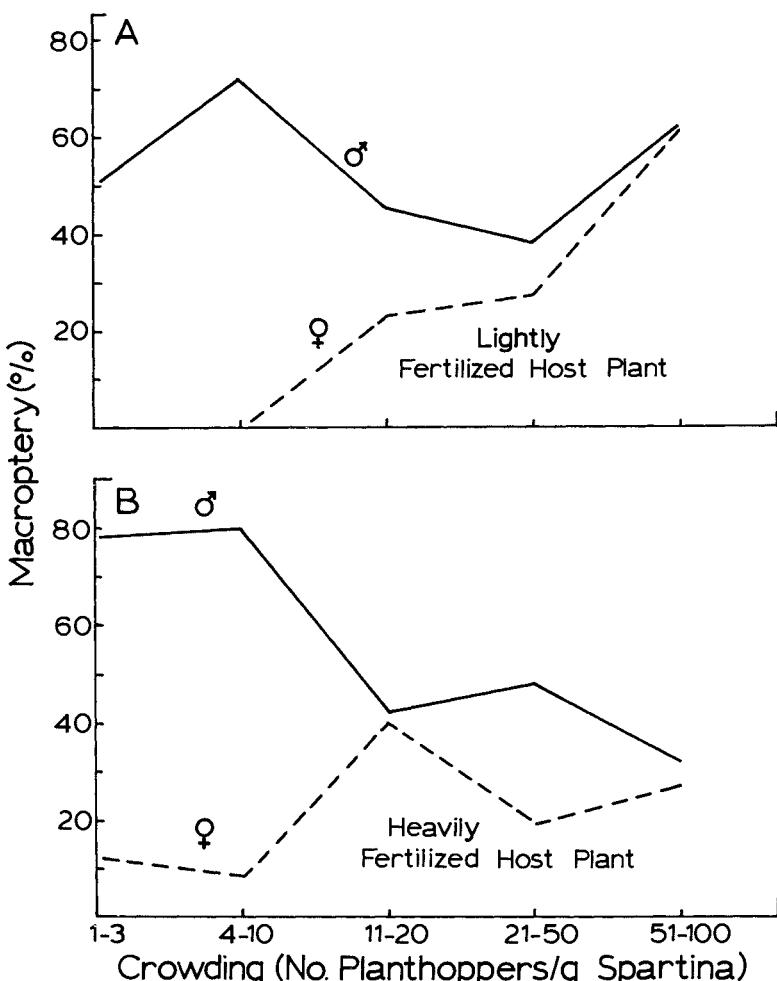
Thus, the production of migratory forms is density-dependent in females, and superior host nutrition dampens the migration response that otherwise occurs in both sexes at high densities on poor quality hosts.

Figure 44.3: Relationship between planthopper load (level of crowding incurred during the nymphal stage) and the adult body length of male and female Prokelisia marginata raised on heavily and lightly fertilized seedlings of Spartina alterniflora. Because the effects of plant nutrition and sex and their interaction on body length were significant (ANOVA), separate regressions for body length and crowding are plotted for all combinations of sex and plant nutrition. The significant interaction between crowding and host plant nutrition (ANOVA) is illustrated by the divergence in body length (y , in mm) of planthoppers raised on nutritionally superior and inferior host plants as crowding (x , number of nymphs per gram Spartina dry mass) increases. For females on superior hosts: $y = 2.72 - 0.0011x$, $n = 26$ cages, $R^2 = 0.014$. For females on inferior hosts: $y = 2.56 - 0.0013x$, $n = 22$ cages, $R^2 = 0.086$. For males on superior hosts: $y = 2.37 + 0.00005x$, $n = 30$ cages, $R^2 = 0.0001$. For males on inferior hosts: $y = 2.31 - 0.0005x$, $n = 23$ cages, $R^2 = 0.031$. Data are means ± 1 SE.



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Figure 44.4: Relationship between the level of crowding incurred during the nymphal stage and per cent macroptery in eclosing males and females of *Prokelisia marginata* raised on lightly fertilized (A) and heavily fertilized (B) seedlings of *Spartina alterniflora*. The soluble protein content of heavily fertilized seedlings ($\bar{X} \pm SD$) was 61.5 ± 7.4 mg/g and of lightly fertilized seedlings 15.5 ± 4.3 mg/g. For males on lightly fertilized hosts, $r = 0.179$, $n = 24$ cages, $P = 0.4015$; for females on lightly fertilized hosts, $r = 0.738$, $n = 22$ cages, $P = 0.0001$; for males on heavily fertilized hosts, $r = -0.268$, $n = 30$ cages, $P = 0.1523$; for females on heavily fertilized hosts, $r = 0.124$, $n = 26$ cages, $P = 0.5449$



Source: From Denno et al. (1985)

Crowding and Host Nutrition in the Field

In this last section of this chapter I extend these laboratory findings on host plant nutrition and crowding to the field in order to understand the underlying mechanisms driving the interhabitat migrations of Prokelisia. Movements between habitats must necessarily be associated with the fitness benefits in the respective patches. Knowing that crowding and host nutrition can affect the fitness of Prokelisia I would like to compare these two factors between the two major habitats of this planthopper - the high marsh and streamside habitats. First let us concentrate on the high marsh habitat. A common pattern on the high marsh is for planthopper density to increase exponentially throughout the season. By mid-summer there can be over 1,000 planthoppers/m². Furthermore, following a high in May, the nutritional quality of Spartina (measured as soluble protein) decreases rapidly (Denno et al., 1985). We may now ask what the consequences are for planthoppers that remain in the high marsh habitat during July when conditions can be crowded on poor quality hosts.

We find that the body length of female Prokelisia is shortest (2.74 mm) during the summer in the high marsh habitat. By migrating to the streamside habitat in early June, Prokelisia is able to realize a much larger body size (2.95 mm) (Denno et al., in preparation). During July and August when nymphs are developing, the soluble protein content of the streamside vegetation is 36 mg/g. This compares with only 21 mg/g for Spartina on the high marsh. This nutritional difference is also confirmed by the fact that the total free amino acid content is always higher in streamside vegetation (Denno et al., in preparation).

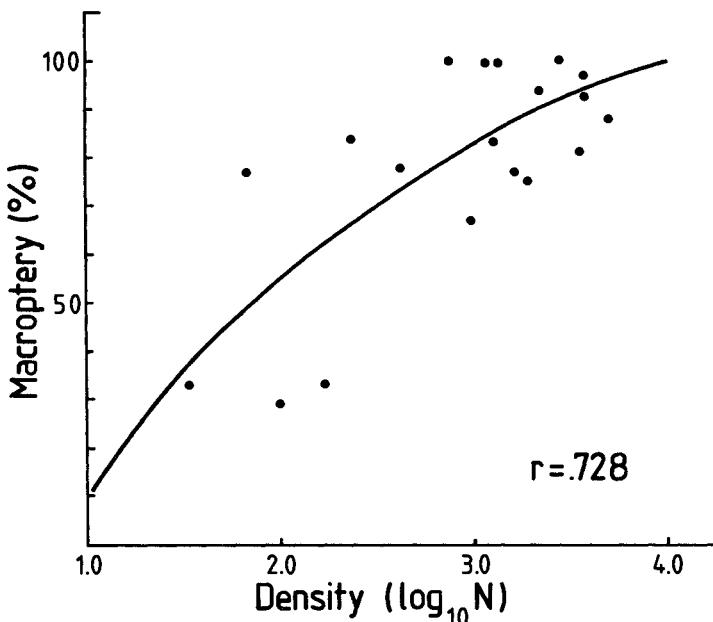
The absolute difference in body size between high marsh and streamside Prokelisia cannot be attributed to temperature because the leaf blade temperature of Spartina is virtually the same between high marsh and streamside habitats at the same time on any given day (Denno et al., in preparation). Both field and experimental data strongly implicate host nutrition as the factor primarily responsible for the larger body size and fecundity of hoppers in streamside vegetation.

Now I confirm by laboratory findings and show that changes in the density of planthoppers and the nutritional quality of Spartina both contribute to wing-form determination in field populations of Prokelisia. To test the effects of density on wing-form in the field, I took seasonal samples and correlated the percentage macroptery in adult female Prokelisia with the density or level of crowding they experienced as nymphs 4 weeks before. There is a positive curvilinear relationship between density and the proportion of macropters as predicted (Figure 44.5).

Results of the greenhouse experiment showed that density-dependent macroptery was damped on superior quality hosts. To manipulate host plant quality in the field, I fertilized large (100 m²) plots of Spartina on the high marsh. Fertilization resulted in a significant increase in the soluble protein content of Spartina culms throughout the season. By August, fertilized plants contained 43 mg/g soluble protein and non-fertilized plants contained only 25 mg/g soluble protein. I also followed changes in the frequency of macroptery in adult females in both control and fertilized plots.

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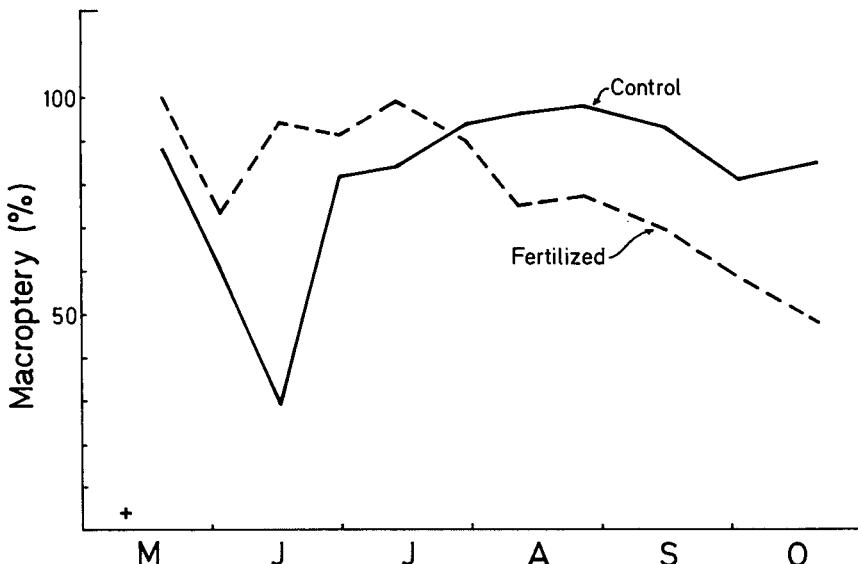
Figure 44.5: Relationship between % macroptery in adult females of Prokelisia marginata and the population density they experienced as developing nymphs. A greater percentage of females molt to potential migrants at high densities. The relationship was generated from data collected at Tuckerton, New Jersey



The frequency of macroptery was higher in the fertilized compared to the control plots through July (Figure 44.6). Independent experiments show that this early season pattern resulted from higher rates of colonization by macropters in the fertilized plots (Denno, 1983). However, after July, the frequency of macroptery in females was significantly less in the fertilized treatment. This late season pattern was the result of an absolute increase in the density of brachypters in the fertilized Spartina (Denno et al., in preparation). These data provide strong field conformation of my laboratory findings that superior host nutrition can dampen the migration response in Prokelisia.

In conclusion, I contend that it is the unique seasonal opportunity to exploit a more nutritious resource that has provided conditions favoring the evolution of migration. The process is mediated by environmental cues like crowding and host plant nutrition that trigger a developmental switch to determine the migratory fate of individuals. Wing-dimorphism is maintained in Prokelisia because brachypters have a reproductive advantage in localized persistent patches of Spartina on the high marsh. In

Figure 44.6: Percentage macroptery in populations of Prokelisia marginata in fertilized and non-fertilized plots of Spartina alterniflora on the high marsh at Tuckerton, New Jersey. Elevated levels of macroptery in fertilized plots during June and July are the result of immigrating macropters. Lower levels of macroptery in fertilized plots during the fall are the result of absolute increases in the brachypterous form. Superior host plant quality dampens the migration response.



these local patches associated with mud pannes, we feel that the proximate nutritional quality of Spartina may be unusually high due to stress-induced increases in the concentration of free amino acids (Denno et al., in preparation).

ACKNOWLEDGEMENTS

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Chapter Forty-five

THE UTILIZATION OF SEAGRASS MEADOWS BY FISHERY ORGANISMS

W.J. Kenworthy, G.W. Thayer and M.S. Fonseca

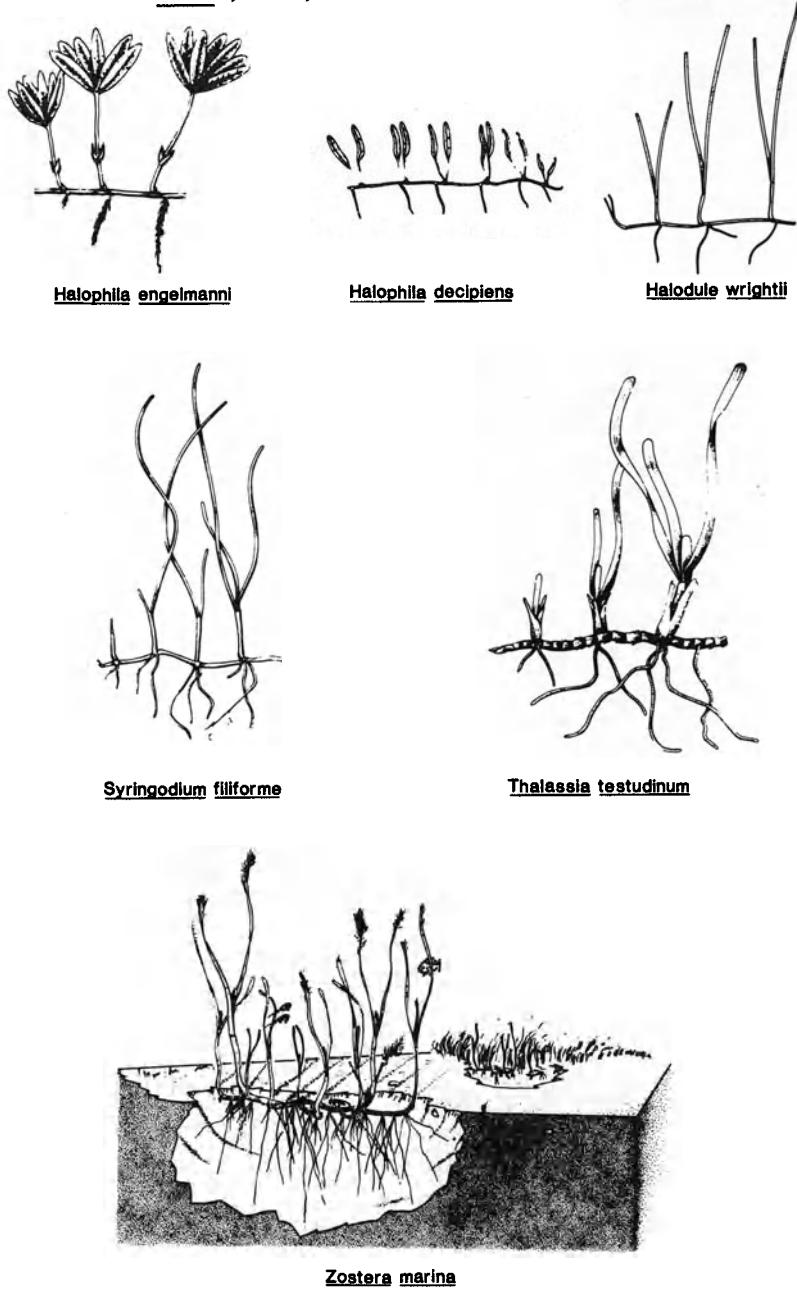
INTRODUCTION

Seagrasses are a closely related group of 50 species of monocotyledonous angiosperms divided between two families and 12 genera which have evolved the characteristics required to colonize successfully the world's shallow coastal zone (den Hartog, 1970). Seagrasses are the only vascular plants that can complete their entire life cycle fully submerged in a saline environment and are distinguished by their erect, linear grass-like leaves which extend from a rhizome that is usually anchored in unconsolidated sediments by an extensive root system (Figure 45.1). To obtain sufficient light energy for photosynthesis these plants grow in relatively shallow water.

Early in this century it was postulated that cod and plaice in the Kattegat region of Denmark were almost entirely dependent on the eelgrass community for their food resources; this hypothesis was tested in the 1930s during and following the demise of eelgrass populations along most of the North American, European and Atlantic coasts. But, the predictions of the model were not as dramatic as expected. The general decline in abundance of organisms important to major commercial and recreational fisheries was not easily recognized, except for a few species. Most notable were declines in the bay scallop, *Argopecten irradians*, which depends on eelgrass blades for attachment of postlarvae. Other fauna living on or among the eelgrass blades showed a less rapid decline (see Phillips, 1984; Thayer, Kenworthy and Fonseca, 1984a). More obvious changes were documented in the physicochemical environment associated with sedimentary and current regimes of the original grass beds (see Thayer et al., 1984a).

After the wasting disease episode there was a period of falling interest in the importance of seagrass, but with general recovery of eelgrass in the 1950s and 1960s, scientific interest has been renewed. During the past decade research has focused upon the functional role that seagrass ecosystems perform in the maintenance of nearshore fisheries production. Many studies have shown that seagrasses occur in shallow water in close proximity to areas where estuarine-dependent, reef resident and temporary residents from deeper water habitats occur at some stage in their life history (Kikuchi, 1980; Zieman, 1982; Thayer et al., 1984a).

Figure 45.1: Illustration of some morphological features of 6 species of seagrass and the multidimensional nature of a seagrass meadow (from Zieman, 1982; Thayer et al., 1984)



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For example, many fish such as grunts, parrotfish, and snappers that are residents of coral reefs by day, are found foraging in seagrass beds at night (Ogden, Brown and Salesky, 1973; Ogden, 1980). Throughout temperate regions juveniles of open water coastal fisheries reside temporarily in estuaries and many frequent seagrass beds (Kikuchi, 1980).

To conserve and utilize the valuable seagrass resources we must understand the distinguishing features of seagrass beds that attract abundant fishery organisms and their food. The characteristics of seagrass meadows that serve in supporting fishery organisms can be broken down into three distinct categories: (1) seagrasses exhibit high rates of primary production which furnish a large source of organic matter; (2) the plant's morphology provides a physically recognizable structure and substrate for refuge and attachment above and below the sediment surface; and (3) the persistence and longevity of a seagrass meadow provide physical and biological stability that promotes both short- and long-term interactions between the meadows and the manner in which they are utilized. These aspects are discussed in detail by Zieman (1982), Thayer et al. (1984a), Fonseca, Zieman, Thayer and Fisher (1983), and Kenworthy, Currin, Smith and Thayer (1987) and will only be discussed briefly.

SEAGRASSES AS A FOOD SOURCE

The conspicuously large biomass frequently observed in seagrass meadows is the result of high rates of net primary production. Representative values for leaves are $0.3\text{-}8.0 \text{ g C}\cdot\text{m}^{-2}\text{d}^{-1}$ for Zostera marina, $0.9\text{-}16.0 \text{ g C}\cdot\text{m}^{-2}\text{d}^{-1}$ for Thalassia testudinum and $0.5\text{-}0.8 \text{ g C}\cdot\text{m}^{-2}\text{d}^{-1}$ for Halodule wrightii and Syringodium filiforme. Where root and rhizome production have been measured, values of $0.5 \text{ g C}\cdot\text{m}^{-2}\text{d}^{-1}$ or less are common (see Zieman, 1982; Thayer et al., 1984a; Kenworthy and Thayer, 1984). Productivities in some seagrass systems approach rates observed in subsidized agriculture crops (Zieman and Wetzel, 1980). Whereas seagrasses in temperate regions exhibit dramatic seasonal cycles, the production of subtropical and tropical seagrasses is relatively constant year round and generally much greater on an annual basis.

These high rates of primary production translate into several features of seagrass systems important to fishery organisms. The leaves of most seagrasses emerge about every 10-15 days (Zieman and Wetzel, 1980); at first growing very rapidly and decreasing exponentially with age. These growth rates result in a high yield of plant biomass, with values usually in excess of 200 g m^{-2} for both leaves and rhizomes of Zostera and in excess of 500 g m^{-2} for each component of Thalassia not uncommon. The conveyor belt-like growth of the leaves on a shoot also produces a very dense and diverse standing crop. Epiphytic organisms attach to the older leaves, and provide additional sources of primary production, perhaps as much as one-third or more of the primary production of the seagrass itself (Penhale, 1977; Morgan and Kitting, 1984). Throughout the entire life cycle of an individual leaf, dissolved organic carbon (DOC) leaches from the plant and is utilized by the

epiphytes (Penhale and Smith, 1977). At the senescing tips of the oldest leaves, bacteria may use virtually all the dissolved organic carbon while reaching their maximum biomass and productivity (Kirchman, Mazella, Alberte and Mitchell, 1984).

The canopy provides a mixed recipe of available organic matter which is utilized primarily in two trophic pathways: (1) directly by herbivores, including the utilization of epiphytic organisms, and (2) indirectly through a complex detrital food web. Few herbivores have evolved the digestive mechanisms to assimilate the ingested seagrass which is composed of a relatively large amount of cellulose and hemicellulose (Kenworthy and Thayer, 1984). But, those organisms which have the digestive tools demonstrate a clear preference for a certain portion of the canopy. For example, in Caribbean seagrass meadows parrotfish (Sparisoma radians and S. chrysoptera) will select the most epiphytized blades (Ogden and Lobel, 1978). On the contrary, the green turtle (Chelonia mydas) appears to prefer the younger and lower portions of leaves that have fewer epiphytes (Zieman, Iverson and Ogden, 1984). The green turtle maintains active grazing patches in a meadow where they constantly recrop the turtlegrass and obtain a diet high in nitrogen and low in fiber (Bjorndal, 1980; Ogden, Robinson, Whitblock, Daganhardt and Cebula, 1983). The manatee (Trichechus manatus) excavates the sediment, removes entire plants, and is one of the few herbivores to include roots and rhizomes in their diet (Thayer, Bjorndal, Ogden, Williams and Zieman, 1984b).

Many of the large herbivores are endangered species and, except for isolated areas, the significance of their grazing is limited. Generally, direct grazing has been considered relatively unimportant, especially in temperate seagrass systems where it is estimated that less than 10 per cent of the seagrass production is consumed directly (see review by Thayer et al., 1984b). This has raised many questions about the functional role of seagrass systems and has fostered research into the role of epiphytes and the detrital food web.

Caribbean seagrass beds are frequented by many feeding generalists. Many urchins feed on seagrass while some species such as Tripneustes ventricosus and Diadema antillarum prefer epiphytized seagrasses (Ogden and Lobel, 1978; Ogden, 1980). The queen conch feeds on both the epiphytes on the blades and on the entire blade, but many temperate and tropical gastropods rely heavily on epiphytes (Huh and Kitting, 1985 and references therein). Thayer, Parker, LaCroix and Fry (1978) concluded that epibiotic community carbon could be derived from DOC released by the seagrass and Kitting, Fry and Morgan (1984) concluded that many of the invertebrates derived their carbon from algal epiphytes. Carnivorous fishes in seagrass meadows may shift their diets to available epiphytic algae during seasonal periods of depleted resources (Kitting et al., 1984).

The major proportion of fresh seagrass material may become available only after it undergoes decomposition. During decay the original plant material leaches labile DOC and is colonized by bacteria, fungi and microfauna which convert a portion of the seagrass into microbial protoplasm and mineralize the remaining

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fractions (see Robertson, Mills and Zieman, 1982). Small microfauna, for example ciliates and protozoans, graze on the bacteria and are thought to enhance their productivity by constant cropping of the microbial biomass (Harrison and Mann, 1975; Fenchel, 1977). Larger fauna, such as nematodes and small crustaceans, may further assist in the breakdown by fragmenting the particles, which in turn exposes larger quantities of surface area to leaching and colonization (Harrison and Mann, 1975; Robertson and Mann, 1980). Through this relatively slow process (see references in Kenworthy and Thayer, 1984) detritus is potentially made available to larger deposit feeding benthic organisms such as polychaetes, amphipods, ophiuroids, gastropods and mullet. Filter feeders and suspension feeders also may consume the very small detrital particles resuspended by water turbulence.

Quantitative estimates of the amount of energy actually transferred to detritivores still remains to be determined. We lack reliable estimates of the microbial production on seagrass detritus and must rely on inferential evidence for establishing the magnitude of this indirect trophic link (Kenworthy, Currin, Smith and Thayer, 1987). An alternative to a microbially mediated food web is one in which the plant debris is consumed and assimilated directly by detritivores. This involves a shorter and perhaps more efficient food chain; however, evidence for its existence is limited. Zieman, Mecho and Mills (1984) reported that pink shrimp, Penaeus duorarum, had a strong reliance on seagrass material or on seagrass-supported trophic intermediaries. Foulds and Mann (1978) determined that a mysid shrimp was capable of digesting cell wall components of vascular plants. Even though the assimilation efficiency of animals for detritus generally is low, the large abundance of litter may actually yield the same nutritional value for an animal as would a high assimilation efficiency for more nutrient rich and easily digested microbes associated with detritus (Hargrave, 1976). More investigations of consumption and assimilation of detritus as well as measurements of attached microbial production are needed.

The influence of seagrass detritus extends well beyond the boundaries of the seagrass meadow. Labile organic compounds leached from living and senescent plant material are transported out of the meadows by currents to be utilized by microorganisms in the water column. The large abundance of particulate seagrass matter is readily noticeable in both temperate (Bach and Thayer, 1986) and tropical systems (Zieman, Thayer, Roblee and Zieman, 1979). Export of particulate debris as drift and bedload from seagrass meadows can exceed 80 per cent of the indigenous plant production.

THE ROLE OF SEAGRASS AS STRUCTURAL HABITAT FOR FISHERY ORGANISMS

Seagrass leaves extend into the water column to form a three-dimensional structure (Figure 45.1). Since there are many co-occurring age classes of leaves and shoots the canopy is multi-layered (Zieman, 1982; Thayer, Kenworthy and Fonseca, 1984a).

Epiphytes attached to the blade surfaces or on the sediment add additional surface area and complexity. Seagrass meadows can appear as a dense, tangled web of leaves or in some instances, a very organized assemblage of neatly spaced shoots. The roots and rhizomes penetrate the sediment, adding a dimension to the meadow achieved by no other submergent marine plant, securing the shoot in place while stabilizing the bottom and providing a protected habitat. These meadows vary in size from small isolated patches of plants a few meters in diameter to vast, continuous distributions many hundreds of kilometers in area (Thayer *et al.*, 1984a).

The surfaces of the leaves exert a frictional drag force which reduces the current velocity and dampens wave motion (Fonseca, Fisher, Zieman and Thayer, 1982; Fonseca and Fisher, 1986). In relatively higher current areas the canopy will bend and compress into a compact layer deflecting water flow over it. Within the environment of a meadow, organic matter and fine-grained sediments tend to accumulate, creating a physicochemical regime distinguished from the unvegetated substrate (see Kenworthy, Zieman and Thayer, 1982; Short, 1983; Thayer *et al.*, 1984a). This generalization cannot be extended to all seagrass meadows, since the hydrodynamic environment of shallow water systems varies over a wide spectrum of energy regimes as does the occurrence of seagrass meadows.

Fonseca *et al.*, (1983) postulated that all seagrass meadows probably do not provide equivalent habitat utilization potential, but that under high current regimes fauna would need special adaptations for clinging to or penetrating the sediment as well as different feeding strategies to accompany the physical changes. In high current areas only small animals are likely to penetrate the dense compressed canopy. These animals would be less conspicuous and more energy would be required of their predators to capture them. In high current areas dominated by patchy seagrass distributions, a greater degree of habitat heterogeneity would exist containing transitional and edge environments that are believed to increase species diversity. In general, however, little is known of how the hydrodynamic regime of seagrass meadows affects the abundance and distribution of animals.

Several faunal surveys in many geographic locations and different types of seagrass habitats indicate that seagrass meadows have consistently greater abundances and higher species diversity than unvegetated areas of shallow water marine systems. Orth (1977) argued that higher densities of infauna in seagrasses were primarily the result of sediment stability, while other investigators have argued that infaunal and epifaunal abundances are the result of habitat heterogeneity, food availability, increased living space and protection from predators (Heck and Whetstone, 1977). Habitat heterogeneity and increased living space have been reasonably well documented as important mechanisms for enhancing faunal abundance (Stoner, 1980). Greater plant biomass and surface area equates with more substrate for the attachment of larvae, shelter for juveniles, and a greater abundance of food resources.

Intricate predator-prey relationships mediated by plant biomass, shoot density, and surface area are important in the organization of seagrass communities (Lewis, 1984). Blade densities

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interfere with the efficiency of foraging predators (Nelson, 1979; Stoner, 1982). The visible detection of prey is inhibited by light attenuation within a canopy and increased blade surface area which camouflages small, cryptic epifauna. Stoner (1980) demonstrated that some amphipods have behavioral affinities for high density seagrass that naturally conceal them. Likewise, there appears to be a strong ontogenetic pattern of feeding by many fishes. The smallest age classes of some species prefer feeding almost exclusively on amphipods, but as they increase in size the dietary importance of smaller crustaceans decreases, the animals tend to become omnivorous and seagrass becomes more abundant in their diets (Livingston, 1982). The high density of shoots and large plant surface area inhibit movement of larger predators more than for juveniles. Many of the larger piscivores, such as sea trout, barracuda, gray snapper, and sharks are visual predators relying on high speed and prey detection which will be hindered by reduced light and high blade density. This is an excellent example of the potential nursery role of seagrass; food availability to juveniles may be unlimited, and as they forage within the canopy they are coincidentally protected from larger predatory carnivores (Stoner, 1982). Consequently, predation pressure, especially by juvenile pinfish, is postulated to be a major mechanism for structuring benthic macrofaunal communities in Gulf of Mexico seagrass habitats.

The dense, interwoven mat of seagrass rhizome also appears to interfere with predation. Peterson (1982) postulated that shallow-dwelling hard clams may be protected by the rhizome layer whereas on an exposed sand flat whelks easily detect and capture clams. Decapod crustaceans, especially crabs (genus Callinectes), however, can readily excavate through or under a seagrass rhizome mat leaving only the very deepest dwelling prey safe from capture (Heck and Orth, 1980). Blue crabs are probably abundant in seagrass meadows for two reasons: (1) juveniles obtain protection from larger predators, while (2) they feed successively on relatively large resources that include both epifauna and infauna (Heck and Thoman, 1984).

SEAGRASS MEADOWS AS A PERSISTENT, LONG-TERM RESOURCE BASE

Several elaborate behavior patterns have been postulated and to some extent demonstrated for seagrass fauna. The timing and complexity of some interactions suggest that long-term evolutionary processes have operated effectively to structure seagrass communities. Based on limited fossil evidence and geological reconstruction of the earth's history, den Hartog (1970) argued that most primitive seagrasses began evolving during the late Cretaceous and Eocene periods. Distinctive animal associations with seagrasses, especially foraminifera and deposit feeding gastropods, can be traced through the geological record (Brasier, 1975). The first fossils of a seagrass herbivore, C. mydas, were deposited during the Miocene. Certainly there has been an adequate period of time

to allow sophisticated interactions to evolve between seagrasses and marine fauna in both temperate and tropical systems.

One of the most important features of seagrass meadows is their longevity and persistence in shallow coastal areas. Where conditions remain unaltered by anthropogenic disturbance or large-scale climatic events, seagrasses tend to persist year after year. Several species, for example *Z. marina* and *H. wrightii*, are capable of rapid recovery rates after a disturbance (Homziak, Fonseca and Kenworthy, 1982; Thayer, Fonseca and Kenworthy, 1985; Fonseca *et al.*, in press) unless the source of disturbance persists as a permanent alteration to the environment.

There are permanent residents of seagrass meadows in temperate and boreal climates but because of the strong influence of seasonality, most are seasonal and are usually dominated by juveniles (Kikuchi, 1980). The seasonality of *Zostera* meadows is evidenced by a drastic decline in density, biomass and canopy surface area during colder winter months (Thayer *et al.*, 1984a). Throughout most of the temperate range of eelgrass and its few congeners (*Ruppia maritima*, *Z. noltii*, *Z. japonica*), the spring and summer increase in plant abundance coincides with periods when many of the estuarine residents and temporary estuarine-dependent fishery organisms are larval, postlarval and juvenile stages (Kikuchi, 1980; Thayer *et al.*, 1984a). Larvae and juveniles of important commercial and sport fish such as gag grouper, snapper, bluefish, mullet, spot, croaker, herrings and many other species appear in *Zostera* beds in spring and early summer. Many of these fish reside only temporarily in the grass bed either to forage, spawn, or escape predation. Some species reside until the fall when they return to the open coastal shelf waters to spawn. The most permanent residents of temperate meadows are typified by tubicolous or burrowing organisms which are more adapted to avoid predation and overwinter in the protection of the sediments (Nelson, 1979). The seasonal rhythms of reproduction and development of many temperate fisheries organisms coincide with the seasonal abundance of seagrass. This does not necessarily indicate that many of the temperate estuarine-dependent species would disappear if eelgrass were removed. Upon removal of the vegetation, however, major sources of primary production, substrate, sediment stability, and shelter would be unavailable.

DIEL UTILIZATION OF SEAGRASS MEADOWS

Nocturnal behavior of fishes and invertebrates are common in tropical seagrass systems, especially those which are close to reefs. Juveniles and adults of many species of reef fish form resting schools on reefs where they find shelter in crevices and caves. At night the fishes migrate from the reefs out onto the surrounding grass beds and sand flats to forage. The significance of this pattern has been revealed through studies of the variation in seagrass fauna over diel cycles. Since there is relatively less environmental and biological seasonality, and reasonably constant recruitment, it has been theorized that the reef-grassbed contact is a good example of highly evolved community resource partition-

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ing (Zieman, 1982). These habitats are efficiently partitioned both spatially and temporally in one of the world's most diverse marine environments. The central role played by the seagrass is to provide, concurrently, food and shelter while providing additional habitat to an already diverse ecosystem of reefs and mangroves (Weinstein and Heck, 1979).

Nocturnal feeders include urchins and spiny lobsters, whereas some fishes, for example parrotfishes and surgeonfish, feed primarily by day (Ogden et al., 1973; Ogden and Zieman, 1977). Ogden et al. (1973) attributed the formation of sparsely vegetated halos around patch reefs to the herbivorous activities of these animals. Near-reef grass beds appear to be exploited by relatively larger fishes while smaller fish range out much farther from the reef. Restricted movement of larger fish is postulated to be controlled by larger carnivores hunting the beds, both by day and night. Smaller fishes are able to range out farther because they can readily seek shelter in the canopy and avoid detection by predators. This is probably the same reason why permanent daytime residents of grass beds in St Croix, US Virgin Islands are generally smaller than reef fishes (Weinstein and Heck, 1979; Roblee and Zieman, 1984).

LARGER ROLE OF SEAGRASS ECOSYSTEMS IN FISHERIES PRODUCTION

On a synoptic scale, seagrass systems appear to play a pivotal role for some major fishery organisms. On the Pacific coast of the United States, herring rely heavily on the blades of eelgrass as a substrate to deposit their eggs. In subtropical and tropical regions the postlarvae of shrimp and spiny lobster recruit into grass beds from distant offshore spawning grounds. Juvenile pink shrimp appear to prefer seagrass habitat but move off into deeper waters as they mature (Zieman, 1982). Lobsters reside in shallow grass beds for about 9-12 months then migrate into deep water and return to grass beds at night to feed. At maturity, usually 1.5-2.0 years, the adult lobsters mate and the females migrate to deep offshore reefs to spawn. The entire cycle is completed with the return of the larvae to shallow grassy areas.

One of the most interesting behavioral patterns for seagrass fauna occurs in the Western Caribbean where large migrations of green turtles annually congregate on the extensive shallow carbonate banks of the eastern Nicaragua coast. The shallow shelf extending some 120 km offshore and south to the Costa Rica border is an expansive seagrass plain dominated by T. testudinum. The shelf is the feeding ground for the turtle population that utilizes the nesting beach at Tortuguero 350 km south in Costa Rica (Ogden, 1980). Food generally is unavailable to the turtles at the nesting beaches, and it is believed they utilize the feeding grounds much as do the migratory populations of ungulates in terrestrial grasslands. The animals migrate to the shelf to feed primarily on seagrass and restock their stores of energy. The turtles feed by day and rest at night at the reefs and rubble interspersed among the meadows. Because of high productivity of

Thalassia and a relatively low food intake, Bjorndal (1985) estimates that the carrying capacity of these seagrass meadows was 138 adult turtles per hectare. In addition, there is little inter-specific competition for the food resource since there are so few herbivores. As mentioned previously, resource partitioning occurs between the fish that prefer epiphytized blades and the turtles that prefer cleaner blades.

SUMMARY

The longevity of seagrass meadows, coupled with their complex physical structure and high rates of primary production, enable them to form the basis of an abundant and diverse faunal community. No other marine plants are uniquely adapted for the position seagrasses occupy in the shallow marine environment. For many fishery organisms there is no one reason why they should be attracted to seagrass meadows but, rather, there are a combination of features providing many essential resources. For some animals the seagrass is primarily a substrate for attachment, but for others such as small cryptic animals and juveniles, food and shelter are obtained simultaneously. Only for a few exceptions do seagrasses provide food directly. The majority of organic matter produced by the plants is either decomposed within the bed or transported to other coastal systems. Direct trophic transfers are minimal but the potential for indirect links through a detritus food web, benthic algae, and epiphytes is enormous.

Very recent quantification of wetland losses and the decline of seagrass in specific estuaries will undoubtedly result in the decline of associated fishery organisms, and a general degradation of estuarine productivity. Fortunately, during past declines seagrasses have recovered naturally in some areas but, should water quality continue to deteriorate, recovery of seagrasses and restoration of their important faunal communities will be limited, if not impossible.

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Chapter Forty-six

A COMPARISON OF FISH AND INVERTEBRATE COMMUNITY COMPOSITION IN TIDAL FRESHWATER AND OLIGOHALINE MARSH SYSTEMS

William E. Odum, Lawrence P. Rozas and Carole C. McIvor

INTRODUCTION

Tidal freshwater wetlands and associated open water are a distinctive type of estuarine ecosystem located upstream from tidal saline wetlands (salt marshes) and downstream from non-tidal freshwater wetlands (Figure 46.1). They are characterized by near freshwater conditions (average annual salinity of 0.5 ppt or below) except during periods of extended drought, but they also have a daily, lunar tidal fluctuation as a result of their position, typically at the upper end of the estuary. In a classification system based on salinity, these wetlands lie between the oligohaline zone and non-tidal freshwater.

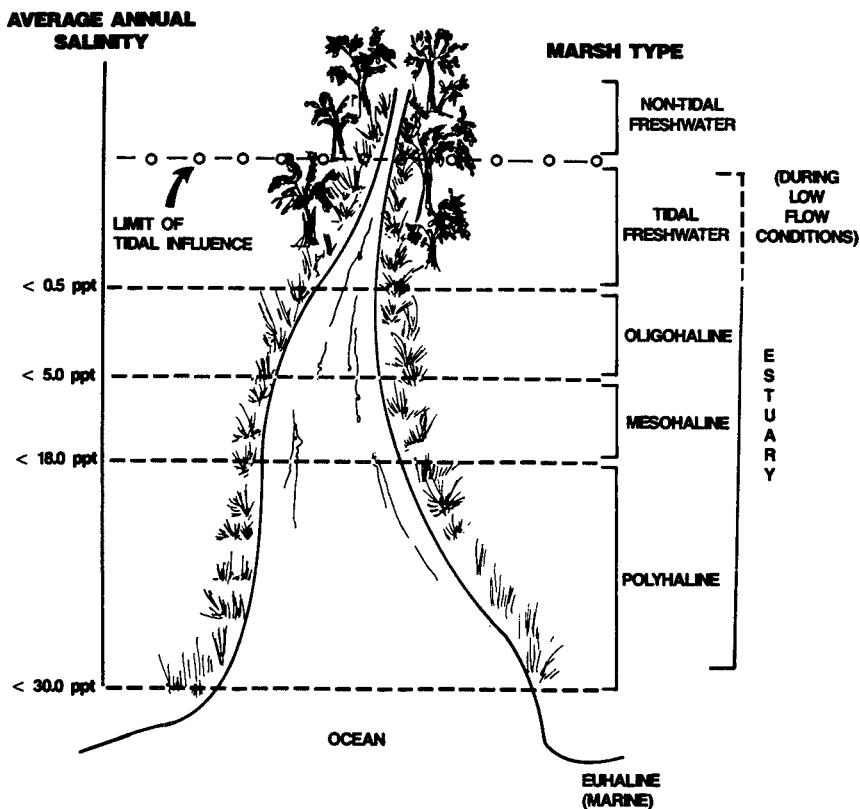
This type of wetland ecosystem is found most commonly along the Atlantic coast of North America and reaches its greatest extent between Georgia and southern New England (see Odum, Smith, Hoover and McIvor, 1984 for a detailed discussion of the distribution in North America). Tidal freshwater wetlands are also found elsewhere in the world such as in western Europe, northern Africa, and southeast Asia. For the purposes of this paper virtually all of our examples and information come from the Atlantic coast of North America. Because tidal freshwater wetlands lie midway between salt marshes and non-tidal freshwater, their animal and plant communities are composed of a mixture of species from both sources. In this paper we analyze the factors which control community composition of invertebrates and fishes.

COMPARISON OF PHYSICAL CONDITIONS

There are major differences between tidal freshwater ecosystems and freshwater and marine ecosystems which lie upstream and downstream, respectively. The most obvious difference is that the salinities in tidal freshwater are much less than those of marine systems. Therefore, the salt stress which affects plants and animals further down the estuary is largely missing, except during occasional periods of extreme drought. The great difference between this environment and non-tidal freshwater is the presence of a daily tidal fluctuation. For many animals and plants this is a major source of disturbance for which they must compensate.

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Figure 46.1: Location of tidal freshwater wetlands on the freshwater-estuarine-marine gradient



Source: From Odum et al. (1984)

Additionally, most habitats in tidal freshwater tend to be characterized by slow-moving water and silty mud bottoms. This creates a relatively low habitat diversity compared to non-tidal freshwater and salt water ecosystems which typically have (1) a variety of bottom types (sandy, gravel, etc.) and (2) different wave and current energy regimes ranging from quiescent waters to high velocity channels.

HYPOTHETICAL TIDAL FRESHWATER ANIMAL COMMUNITIES

Given conditions of low salinity, tidal fluctuations and low habitat diversity, it is probable that only certain species from the non-tidal freshwater and salt water ecosystems will be successful in colonizing tidal freshwater. Since osmotic adjustment is probably

the single most difficult problem for aquatic animals to overcome, this should have the greatest influence on species composition in tidal freshwater.

The species abundance-salinity curve of Remane (1934) has been redrawn by Deaton and Greenberg (1986) as shown in Figure 46.2. This relationship, which is based largely on invertebrate species data, suggests that the aquatic animal communities in tidal freshwater should be composed mostly of freshwater species, fewer brackish water species and virtually no marine species.

Moreover, tidal fluctuation of a meter or more on the east coast of the United States should negatively affect the occurrence of freshwater species that depend on a shallow littoral zone. For example, fishes which nest in very shallow water would be unsuccessful in tidal environments which left their nests exposed for several hours at low tide.

Finally, the limited habitat type which is available (generally silty muddy bottoms), may further restrict the occurrence of species which need sandy or gravel bottoms or other hard substrates for habitat or spawning.

In summary, prior to examining any data, we would expect the tidal freshwater fish and invertebrate community to be extremely limited in number of species by this combination of intermediate salinity, tidal fluctuation and low habitat diversity. Reman's hypothetical salinity relationship further suggests that the overwhelming majority of species in tidal freshwater should be of freshwater origin and that marine species should be virtually absent.

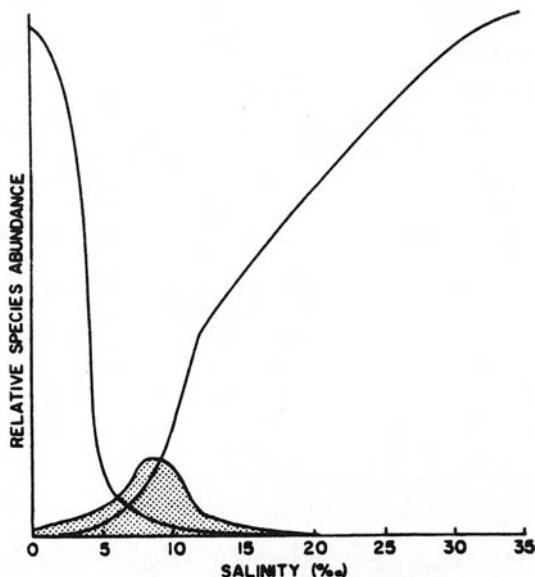
TIDAL FRESHWATER INVERTEBRATE COMMUNITY

The modest amount of information which is available concerning tidal freshwater invertebrates (reviewed by Odum et al., 1984), follows Remane's (1934) predicted species curve very closely. For example, the zooplankton community is composed largely of freshwater ostracods and copepods along with a few brackish water species and virtually no marine species. The benthic community both on the stream bottoms and on the marsh surface is dominated by freshwater species of oligochaetes, amphipods and insect larvae, particularly from the family Chironomidae. Whereas there is a low number of brackish water species such as caridean shrimp, amphipods, and crabs, there are almost no marine invertebrate species present in tidal freshwater. One exception is the blue crab (Callinectes sapidus), a species which some consider estuarine and others marine since it spawns at the mouth of the estuary in salinities close to that of sea water, but spends most of its life within the estuary. In the southeastern United States, certain penaeid shrimp such as the white shrimp (Penaeus setiferus) may move into tidal freshwater during the early stages of its life history (Odum et al., 1984).

In general, however, the tidal freshwater invertebrate community on the east coast of the United States is composed largely of freshwater species with a few brackish water species. Species diversity compared to non-tidal freshwater is considerably reduced

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Figure 46.2: The species abundance-salinity relationship.
Freshwater species are represented by the curve on the left, marine species by that on the right, and brackish water species by the shaded area.



Source: Redrawn by Deaton and Greenberg (1986) from Remane (1934)

(Kirk, 1974; Diaz, 1977). This reduction in invertebrate species in tidal freshwater has been attributed to the combination of low habitat diversity and stress from low salinities (Diaz, 1977).

TIDAL FRESHWATER FISH COMMUNITY

We have examined studies from 13 tidal freshwater estuaries on the east coast of the United States. These include the Hudson River, New York (Perlmutter, Schmidt and Leff, 1967), Woodbury Creek, New Jersey (Hastings and Good, 1977), Delaware River tributaries (Smith, 1971), Potomac River, Virginia (Powell, 1977), Rappahannock, Virginia (Massman, Ladd and McCutcheon, 1952), Pamunkey River, Virginia (Massman et al., 1952), James River, Virginia (VIMS, 1978), Chickahominy River, Virginia (McIvor, Rozas and Odum, in press), Winyah Bay, South Carolina (N. Roark, personal communication), Savannah River (Hornsby, 1982), and Altamaha River, Georgia (Holder, 1982). We have selected the eight numerically dominant species from each of these studies, and classified the fishes as freshwater, estuarine, marine, or anadromous based upon their spawning location. The combined results of this analysis are shown in Table 46.1. These data suggest that the

Table 46.1: Numerically dominant species in tidal freshwater fish communities according to spawning location. Compiled from 13 studies on the US east coast (see text for details)

	%
Freshwater species	60
Anadromous/semi/anadromous	20
Estuarine species	13
Marine species	7

Table 46.2: Dominant fish species found in tidal freshwater on the United States east coast. fw = freshwater species, e = estuarine, m = marine, a = anadromous

Mummichog (<u>Fundulus heteroclitus</u>)	(e)
Banded killifish (<u>F. diaphanus</u>)	(f)
Tidewater silversides (<u>Menidia beryllina</u>)	(e)
Spottail shiner (<u>Notropis hudsonius</u>)	(f)
Blueback herring (<u>Alosa aestivalis</u>)	(a)
Redbreast sunfish (<u>Lepomis auritus</u>)	(f)
Spot (<u>Leiostomus xanthurus</u>)	(m)
Bluegill (<u>L. macrochirus</u>)	(f)
Yellow bullhead (<u>Ictalurus natalis</u>)	(f)

Source: From Odum et al. (1984)

dominant species in tidal freshwater are freshwater species with appreciable numbers of brackish water and anadromous species. Marine fish species tend to penetrate farther into freshwater than invertebrates. Typical examples include the mullet (Mugil cephalus), and the spot (Leiostomus xanthurus). Examples of the dominant species from these various tidal freshwater environments are shown in Table 46.2.

We made a similar analysis of data from oligohaline (annual average of 0.5–5.0 o/oo) waters using the data of Rozas and Hackney (1984), Rounsefell (1964), Gunter and Shell (1958) and Dahlberg (1972) (Table 46.3). The oligohaline fish community, which may be geographically very close to the tidal freshwater fish community, is dominated by estuarine and marine species (Rozas and Hackney, 1983). Whereas anadromous species are periodically present in this environment, they are not typically dominant. Comparison of Tables 46.1 and 46.3 suggests that there is a steep transition with much species turnover in oligohaline and freshwater habitats.

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Table 46.3: Dominant species in oligohaline fish communities based on spawning location

	%
Freshwater species	26
Anadromous/semi-anadromous	0
Estuarine species	33
Marine species	41

Table 46.4: Fishes utilizing tidal freshwater as nursery grounds

Species	Anadromous	Affinity group	
		Marine	Estuarine
Alewife	+		
American shad	+		
Atlantic menhaden		+	
Atlantic sturgeon	+		
Bay anchovy			+
Blueback herring	+		
Gizzard shad	+		
Hogchoker			+
Naked goby			+
Shortnose sturgeon	+		
Southern flounder		+	
Spot		+	
Striped bass	+		
Tidewater silverside			+
White perch	+		
Yellow perch	+		

Source: From Odum et al. (1984)

FISHERIES IMPLICATIONS

A number of freshwater, estuarine, marine and anadromous fishes and invertebrates utilize the tidal freshwater environment as a nursery area (see Table 46.4). There is a resulting large sport fishery in most tidal freshwater areas for a variety of fishes including largemouth bass, striped bass, white perch, catfish and many species of sunfishes. Commercial fisheries are less important in tidal freshwater since many species move downstream into the estuary before they are large enough to harvest. Nevertheless, commercial catches do come from tidal freshwater (Table 46.5).

tfish (brown bullhead, white and channel catfish)	138,872
riped bass	34,211
erican eel	28,028
erican shad	18,203
ite perch	5,449
rp	5,064
ewife and blueback herring	1,121
llow perch	754
appies	187
ckory shad	22
tal	231,911

: From Lippson et al. (1979)

USIONS

mary, the tidal freshwater fish community is dominated by ater species but contains an appreciable number of anadro-nd estuarine species. Marine species invade this area of the γ to a greater degree than predicted by Remane's (1934) esis. This discrepancy probably exists because fishes are obile than invertebrates which Remane used for his hypo-l relationship. It is interesting to note that the oligohaline mmunity, which is not far removed in distance from the tidal ater fish community, is strikingly different in composition. ntly, most marine and brackish water species are better exploit the lowered salinity conditions in oligohaline waters he almost totally freshwater conditions of tidal freshwater. data are consistent with Deaton and Greenberg's (1986) ions that the most severe changes in ionic ratios, a possibly ; factor to invading species, occur in the range of 0-2 ppt than in the range between 5 and 8 ppt as suggested by vich (1969).

nally, it should be noted that most of these examples come emperate latitudes. The data of Rogers, Targett and Van 1984) from Georgia and Lewis, Gilmore, Crewz and Odum from Florida suggest that below latitude 25-30° the use of reshwater by estuarine and marine species may be more nt.

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Chapter Forty-seven

PATTERN AND PROCESS IN ARID-REGION SALT MARSHES - SOUTHERN CALIFORNIA

Christopher P. Onuf and Joy B. Zedler

Salt marshes of the moist eastern United States have been long and often the subject of studies of ecosystem function. In comparison, ecological investigations of arid-region salt marshes are recent and limited. This review relies primarily on research from the last decade in southern California. The results contradict several paradigms of ecosystem function that have emerged from research in the eastern United States. Key differences in the salt marshes between the regions provide insights about the governing process.

CLIMATE

The average annual precipitation of the southern California coastal region is less than 40 cm (Baldwin, 1973). Other coastal areas of the United States average more than twice as high, with the exception of southernmost Texas (60 cm) and central California (80 cm). The temporal distribution of precipitation exacerbates the effect of limited water supply on plant life. Over 80 per cent of the annual precipitation falls between November and April, when temperatures are 4°C lower than May through October and solar energy in the photosynthetically active region is 40 per cent less than in May through October. Among years, precipitation is more variable in southern California than any other region of the United States, especially other coastal regions.

In many regions, terrestrial runoff may exert a stronger influence on the hydrological environment of salt marshes than local precipitation. Storage in snowpack can delay and concentrate peak runoff; groundwater recharge during storms and gradual release during ensuing dry periods can prolong the supply of fresh water to estuaries and their fringing marshes. Thus, substantial flows occur throughout the growing season (April through September) in all the major rivers of the eastern half of the United States. Neither snowpack nor gradual release of ground water moderates streamflow irregularity in southern California. Even in an exceptionally wet year, substantial streamflow persists only a few days after a storm. Although temperatures and rates of evaporation along the coast are moderate, average pan evaporation exceeds precipitation except in January, and after March, monthly saturation deficits exceed 10 cm.

COMMUNITY STRUCTURE AND DYNAMICS

Spatial patterns

The marshes of the southeastern United States are characterized as having a strongly developed zonation with the tall form of Spartina alterniflora occupying creek banks and the short form dominating the interior at low elevations. At higher elevations, Juncus roemerianus replaces Spartina alterniflora, and above that meadows of Spartina patens occur (Reimold, 1977). Toward the upper limit of short Spartina alterniflora, in the vicinity of mean high tide and where soil salinities tend to be highest, a narrow zone of open sand or sparse mixtures of short Spartina alterniflora, Salicornia spp., Limonium spp. and Distichlis spicata can occur (Cooper, 1974).

Zonation is not correspondingly strong in marshes of the Pacific southwest, but there are differences between marshes depending on the degree of tidal flushing (Table 47.1). In wetlands where tidal flushing is common, Pacific cordgrass (Spartina foliosa) is present and tends to occur closest to the fringing intertidal flats or lowest on the banks of tidal creeks. However, elevations of lower and upper marsh vegetation at Tijuana Estuary overlap broadly. Sampling stations with Spartina had the same modal 10 cm elevation class as those inland of Spartina (Zedler and Nordby, in press). In wetlands where tidal flows are often excluded, Spartina is absent, and monotypic pickleweed (Salicornia virginica) dominates the seaward edge.

Landward of this loosely construed lower marsh zone, species tend to reach their peak frequencies of occurrence at different elevations, but are broadly distributed along the elevation gradient (Zedler, 1977; Eilers, 1981). Above the Salicornia fringe at Mugu Lagoon, Onuf (unpublished observations) found four species on average in samples as small as 0.06 m², with weak negative associations between the dominant (Salicornia virginica) and most other species, and positive associations among some of the less-common species. Although several species are likely to co-occur, there is no predicting which they will be. In most marshes, succulents are at least as important as other vascular plants in occurrence, biomass (Table 47.1), and productivity (Zedler, 1977; Eilers, 1981; Zedler and Nordby, in press; Onuf, unpublished observations). Biomass distribution is also very patchy. The coefficients of variation of biomass computed for these marshes range from 37 to 121 (Table 47.1). This is more than twice that measured by Nixon and Oviatt (1973) for 12 Spartina alterniflora marshes in Rhode Island (c.v. range = 11 to 27).

Temporal patterns

Variation in species composition and biomass is temporal as well as spatial. In four years of sampling the low marsh Salicornia virginica zone at six locations successively farther from the mouth of Mugu Lagoon, there were no significant differences in mean biomass at the time of peak standing crop among years or locations. However, there was a significant years x location interaction. A pattern of biomass declining with distance from the mouth

Table 47.1: Characteristics of the vegetation of southern California salt marshes. Species occurring in at least 1% of the samples taken in a marsh are included.

	Well flushed				Tidal flushing impaired			
	Upper Newport Bay	Sweetwater River Estuary	Tijuana Estuary	Mugu Lagoon	Bolsa Bay	Penasquitos Lagoon	Goleta Slough	Carpinteria Slough
% Contribution to total biomass or productivity								
<u><i>Salicornia virginica</i></u> ^a	25	39	16	61	26	72	94	93
<u><i>Frankenia grandifolia</i></u>	2	22	6	39	26	2	5	5
<u><i>Distichlis spicata</i></u>	8	3			23			2
<u><i>Spartinafoliosa</i></u>	27	6	25		12			
<u><i>Jaumea carnosa</i></u> ^a	7	6	20	15				
<u><i>Batis maritima</i></u> ^a	7	7	9	3				
<u><i>Monanthochloe littoralis</i></u>	11	2	18					
<u><i>Limonium californicum</i></u>	5	4		11				
<u><i>Salicornia bigelovii</i></u>	2	4	8					
<u><i>Triglochin maritima</i></u>	5	3		3				
<u><i>Suaeda esteroa</i></u> ^a	1		3					
<u><i>Lolium perenne</i></u>					2			
<u><i>Cotula coronopifolia</i></u>			4		1			
Not separated								
Number of species per sample unit	6.0	5.7	4.4	3.1	2.2	1.4	1.4	1.3
Area of sample unit (m^2)	0.7	0.7	0.25	0.06	0.7	0.7	0.06	0.06

Table 47.1 (continued)

Coefficient of variation for biomass distribution	52	58	44-76 ^b 37-53 ^c	121	41	44	39
Source	1	1	2,3	4	1	1	6

Notes: a, succulent.

b, range of determinations over 5 years in the lower marsh Salicornia zone.

c, range of determinations over 5 years in the upper marsh mixed assemblage.

Source: 1, Eilers (1981); 2, Zedler (1977); 3, Winfield (1980); 4, Onuf (unpublished observations); 5, Onuf (1983); 6, Onuf (1984).

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was strongly evident in 1978. That pattern disappeared gradually in subsequent years, and a weak trend of biomass increasing away from the lagoon mouth was apparent in 1981 (Onuf, in press). Storms causing unprecedented deposition of sediments in the lagoon and salt marsh occurred in 1978 and 1980.

In the one location where the mixed upper marsh was sampled as well as the monotypic lower marsh, the 5-year (1977 to 1981) trend in biomass for the upper marsh was essentially a mirror image of the trend in the adjacent Salicornia virginica zone. Mean biomass was not significantly different over time or between locations (upper versus lower marsh); however, the years x location interaction was significant. In the first 3 years, biomass averaged 40 per cent higher in the upper marsh, while in the last 2 years biomass was 37 per cent higher in the lower marsh (Onuf, in press). Salicornia biomass in the upper marsh was highest in 1978 and declined progressively to 35 per cent of that level by the last year. Jaumea carnosa biomass increased twofold during the 5 years of observation. Other species were too variable or too rare to ascribe pattern.

Sediment deposited by the major storms of 1978 and 1980 was probably responsible for most of the observed changes in the salt marsh vegetation (Onuf, in press). In the lower marsh, sites near the mouth were initially well-drained relative to those far from the mouth. Mud deposits might have been detrimental to the vegetation of well-drained sites and beneficial to plants growing at water-logged sites. By this same logic, accretion in the upper marsh might favor species other than Salicornia virginica.

Long-term vegetation monitoring at Tijuana Estuary (Zedler and Nordby, in press), has spanned an even wider range of environmental conditions than the observations at Mugu Lagoon. Every year at Tijuana Estuary, there is high variability among sampling stations located at 5-m intervals within individual transects. Standard errors for soil salinity are generally less than 10 per cent of the mean. For Spartina height and density, and for cover of other species, standard errors are generally less than 5 per cent of the mean (Zedler, 1983). Nevertheless, stations that are only 5 m apart can have values that differ several fold (Zedler, unpublished monitoring data). The small-scale patterns for Spartina can be explained only by evaluating historical conditions of each quadrat. Correlation coefficients of height, density, and total stem length with 13 environmental factors (e.g. elevation, soil organic matter, cover of other species) were never more than 0.3 (Zedler et al., in press). Multiple regression analysis explained less than 30 per cent of the variation in station-to-station data on Spartina. The strong relationships were with prior conditions. Large increases in Spartina density from 1979 to 1980 were highly correlated with densities in 1979 (r values up to 0.93 for stations along individual transects); heterogeneity was maintained by vegetative growth. Decreases in density, however, were not predictable, resulting mainly from debris that was deposited in patches. Thus, yearly changes in growing conditions and extreme flooding events maintain variability at the level of individual stations.

In the lower marsh, percentage occurrence and total length of Spartina foliosa stem per m² (shoot density x mean height) were measured as non-destructive indicators of biomass, whereas percentage occurrence and percentage cover were used for Salicornia virginica. Percentage occurrence was high and varied little for Spartina between 1979 and 1983, then declined in 1984 and again in 1985. The total length of stems per m² in plots where Spartina was present peaked in 1980 and again at an even higher level in 1983, then declined by more than 90 per cent over the next two years (Figure 47.1). Local rainfall did not explain the pattern; however, the peaks coincided with exceptionally high streamflows into the estuary (>20 times the annual mean for 1937-1977). The estuary was nearly always open to tidal flushing throughout this 46-year period, but in April 1984 the mouth closed and remained closed until it was bulldozed open in December. Rainfall and streamflow were negligible in this period. Soil salinities reached levels more than twice the maximum measured in the preceding five years of the monitoring program, when the mouth was open. The depth to the water-table increased from 30 cm in May to more than 75 cm in October.

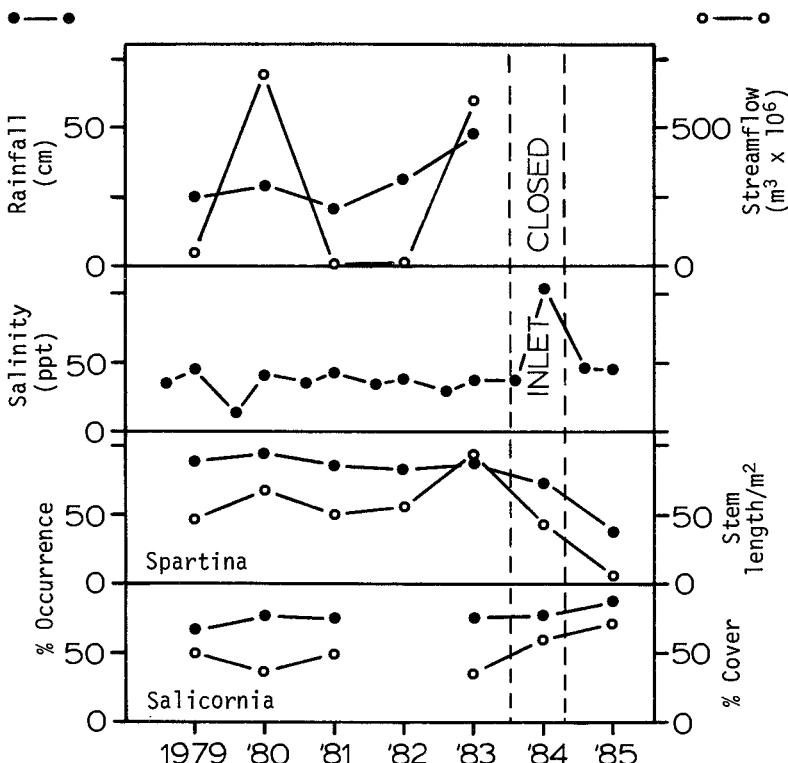
Salicornia responded essentially the opposite of Spartina, with percentage cover decreasing in the high-flow years and then increasing to maximum levels in 1984 and 1985. Salicornia is tolerant of salinity and drought stress, whereas Spartina capitalizes on infrequent flood flows during the growing season.

For the upper marsh mixed succulents assemblage, a survey was conducted in 1974 (Zedler, 1977), but monitoring did not begin until 1984 (Covin, Marsh and Zedler, 1986). Several species that were common in 1974 were absent or rare in 1984 (Table 47.2). After only one non-tidal growing season, the Tijuana Estuary salt marsh declined from one of the most diverse to a succulent monotype characteristic of systems with long histories of modification and restricted tidal exchange. Further declines were evident in 1985 for most species, while Salicornia virginica expanded (Table 47.2).

Thus, the pattern is for the most-tolerant species, Salicornia virginica, to form extensive stands in wetlands that have recently or historically been closed to tidal flushing. Even Salicornia may die out in wetlands with poor tidal flushing if inundation is greatly prolonged; however, it is capable of reestablishing from seed even under highly saline conditions (Zedler and Beare, in press). Reviewing aerial photographs spanning 50 years, Ferren (1985) documented die-back and subsequent recovery of Salicornia over approximately half the area of Carpinteria salt marsh. The period of die-back coincided with virtually permanent closure of the mouth. Recovery occurred rapidly after the local flood control agency stabilized the mouth to insure free exchange with the ocean. Tolerance to high salinity and drought plus ability to reestablish from seed under a wide range of salinities make Salicornia virginica the persistent dominant in marshes with poor tidal flushing.

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Figure 47.1: Characteristics of the environment and the lower marsh vegetation at Tijuana Estuary, 1979-85: annual precipitation; annual streamflow; interstitial soil salinity in April and September; % occurrence and total stem length per m² of *Spartina foliosa*; % occurrence and % cover of *Salicornia virginica*. Precipitation records are from the National Weather Service for Chula Vista. Tijuana River flow is for the USGS gauge at the international border. Flooding was restricted to winter months in a 100-year event in 1980; flows were prolonged by reservoir discharge through the 1983 growing season.



PRODUCTIVITY

There are many published determinations of salt marsh vascular plant productivity for southern California; however, the methods of determination are varied, and the results are generally unreliable for the prevailing conditions of year-round growth and high spatial heterogeneity (Onuf and Quammen, in press). By default, therefore, we are forced to use end-of-season live (peak) biomass as the indicator of productivity in the region.

Table 47.2: Changes in species composition at Tijuana Estuary salt marsh. Data for 1974 are from Zedler (1977). Data from 1984 and 1985 are from the same quadrats. From Covin et al. (1986)

	Frequency (%)			Mean percentage cover ^a	
	1974	1984	1985	1984	1985
<u>Salicornia virginica</u>	69	75	81	59	66
<u>Batis maritima</u>	51	38	32	40	24
<u>Jaumea carnosia</u>	55	24	5	36	9
<u>Frankenia grandifolia</u>	49	26	21	28	16
<u>Triglochin concinnum</u>	9	16	2	32	5
<u>Distichlis spicata</u>	13	4	5	4	5
<u>Monanthochloe littoralis</u>	41	16	12	52	54
<u>Salicornia subterminalis</u>	18	10	7	41	26
<u>Limonium californicum</u>	10	5	1	11	7
<u>Spartinafoliosa</u>	See Figure 47.1				
<u>Salicornia bigelovii</u>	64	0	0		
<u>Suaeda esteroa</u>	37	1	1		
Number of quadrats:	357	216	216		

Note: a, Cover was averaged for quadrats where each species occurred; zeros were omitted

Whole marsh values for peak biomass range threefold, from 500 to 1500 g dry weight per m² (g/m²). (Table 47.3A). Peak biomass was highest in two marshes where tidal flushing was either reduced in some parts by diking (Goleta Slough) or restricted during much of the growing season by a sand bar (Los Penasquitos Lagoon). Two of the three low values were for fully tidal marshes. The third low value may be artefactual, considering the low sampling effort along just one transect (Bolsa Bay). Although tidal action has been postulated to 'subsidize' productivity in eastern salt marshes (Odum, 1980), the probable explanation for a contrary pattern here is the prevalence of stressful, high soil salinities during much of the growing season in tidally dominated systems. Where the tidal influence is weak, low soil salinities will persist much longer into the growing season in years of high or unusually late rainfall, protracting the period of rapid growth. Indeed, the years of measurement were exceptionally wet ones at Goleta Slough (second wettest in 116 years, monthly precipitation exceeding monthly evaporation through April) and at Los Penasquitos Lagoon (twice the long-term mean annual precipitation, mouth closed before cessation of freshwater runoff).

According to this interpretation, differences in peak biomass and presumably production between well-and poorly flushed tidal marshes are more in response to freshwater inputs than marsh-

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Table 47.3: Peak biomass (g/m^2) as an indicator of production in southern California salt marshes. A. Whole-marsh means (\bar{x}), with their standard errors (se) and sample sizes (n). All determinations were made in 1978 except Carpinteria Slough (1984) and Goleta Slough (1983). B. Peak (August) biomass in different years. Sources of data are listed at the bottom and by corresponding reference number in parentheses in the table.

	\bar{x}	se	<u>n</u>	
A				
<u>Well flushed</u>				
Tijuana Estuary (1)	953		25	
Sweetwater River Estuary (2)	984	177	31	
Upper Newport Bay (2)	690	72	25	
Mugu Lagoon (3)	648	60	40	
<u>Tidal flushing impaired</u>				
Los Peñasquitos Lagoon (2)	1500	136	21	
Bolsa Bay (2)	688	373	5	
Carpinteria Slough (4)	871	80	18	
Goleta Slough (5)	1271	98	32	
	1976	1977	1978	1979
	1980	1981		
B				
<u>Well flushed</u>				
Tijuana Estuary: (1)				
whole marsh (mixed)	858	1153	953	
Mugu Lagoon: (3)				
lower zone (<u>Salicornia</u>)	455	464	337	
upper zone (mixed)	503	751	666	
			484	
			590	
			507	
			458	
<u>Seasonally blocked</u>				
Los Peñasquitos Lagoon: (6)				
lower zone (<u>Salicornia</u>)	2666	4316		
upper zone (<u>Frankenia</u> , <u>Distichlis</u>)	1879	1458		

Notes: a, Mouth blocked seasonally by a sand bar.

b, Water exchange at all sample sites affected by a flow control structure.

c, Water exchange to parts of the marsh affected by dikes and flow control structures.

Source: (1) Winfield (1980); (2) Eilers (1981); (3) Onuf (unpublished observations); (4) Onuf (1984); (5) Onuf (1983); (6) Zedler et al. (1980)

specific differences in production potential. Conditions within tidally dominated marshes vary from place to place and year to year, depending on the amount and timing of freshwater input among other things. Tidal inundation puts limits on the range of variation except in the uppermost fringe of the marsh. The tolerances of the species in the mixed assemblage are different enough that conditions depressing the growth of one species will enhance the growth of another, thereby damping fluctuation in total biomass and production. In contrast, marshes with reduced tidal influence experience a wider range of conditions than occur in tidally dominated systems, ranging from prolonged salubrious in wet years to more stressful hypersaline in drought years. Since marshes with reduced tidal flushing tend to be dominated by a single species, there is no buffering of total production and biomass by compensatory responses of different species.

The responses of the salt marsh at Tijuana Estuary to extreme conditions before and after mouth closure dramatically illustrate this conceptual model of primary production in the region's salt marshes (Figure 47.1), however, the measures of Spartina stem length and Salicornia cover do not adequately express the effects on total biomass. Only one direct comparison of biomass with and without good tidal exchange addresses this hypothesized response. In 1978, when precipitation at Los Peñasquitos Lagoon was twice normal, August live biomass was significantly higher (62 per cent) in the low marsh than in 1977, a year of normal precipitation (Zedler, Winfield and Williams, 1980). At the tidal Mugu Lagoon, precipitation was also twice normal in 1978 and normal in 1977, but August biomass in the lower marsh was not significantly higher (2 per cent) in 1978 than in 1977 (Onuf, in press). There is somewhat better documentation of the relative stability of peak biomass in well flushed marshes in the face of great variation in rainfall (Table 47.3B, normal rainfall in 1977 ranging to more than twice normal in 1978 and 1980).

CONCLUSION

Southern California salt marshes are dynamic in both their species composition and productivity. When minor changes in rainfall, temperature, or salinity occur, plants increase or decrease photosynthesis or growth. With larger differences in growing conditions, mortality or reproductive events (through seedling establishment or vegetative spread) may occur. Where species co-occur, the response of one may compensate for the response of others, such that major swings in total productivity and plant cover are ameliorated. The strong effect of the physical environment on the salt marsh is expressed in year-to-year shifts in the distribution of biomass spatially and among species. The largest variations are found in systems where tidal flushing is impaired or absent (Zedler et al., 1980; Ferren, 1985). Large swings in environmental conditions develop when the wetland closes off to tidal flushing. Salinities can range from zero to several times sea water, moisture conditions shift from drought to prolonged inundation, and the changes can be very rapid. In contrast, the well-flushed wetlands

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are buffered by daily tidal exchange. Even in well-flushed marshes, however, there are seasonal patterns of prolonged exposure that lead to rapid drying and increased interstitial salinity.

Rapid change is the feature that continually emerges out of this review of what we know or infer about the structure and function of arid southern California's coastal marshes. Although the description diverges from the paradigms of salt marsh ecosystem function that have evolved out of the decades of research conducted in the estuarine marshes of the southeastern United States, the striking differences can be viewed as logical consequences of the equally striking differences in the climates and physical settings of the regions. In fact, many of the features described for southern California marshes are present in marshes of the southeast, only as a minor, usually overlooked part rather than the whole. It is as if the narrow zone at the upper reach of normal tides in the southeast has been stretched out by the drier conditions of the southwest to cover the whole marsh. Six of the seven species and all the genera listed by Reimold (1977) as characteristic of salt flats in the eastern USA are common in southern California. The lower cover implied in the name salt flat is in keeping with the relatively low biomass and high spatial heterogeneity in the distribution of biomass (frequent bare spaces) so evident in southern California marshes. We are aware of no reports of year to year variability in species composition or biomass for this zone in eastern marshes. On the basis of the equable precipitation regime, we would anticipate low variability; however, the upper reach of the tides is where flotsam deposition is concentrated, which will create patches unpredictably in space and time.

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