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Competition and Allelopathy in Aquatic Plant Communities

Author(s): Brij Gopal and Usha Goel

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Competition and Allelopathy  
in Aquatic Plant Communities

BRIJ GOPAL AND USHA GOEL

*School of Environmental Sciences  
Jawaharlal Nehru University  
New Delhi 110067, India*

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### Abstract

The paper reviews the published literature on the studies of competition and allelopathy in aquatic plant communities. Taking a broader view of the community, the studies on interactions between macrophytes and microphytes, macrophytes and macro-invertebrates and microbial communities are also reviewed. The role of these interactions in the structure and dynamics of aquatic communities has been discussed in light of the current hypotheses concerning competition in terrestrial communities. The available information suggests that the aquatic plants of various growth forms differ greatly among themselves in their responses and adaptations to competition and allelopathy. The possible application of these interactions in biological control of plant pests and in agriculture is also summarized.

We conclude that the observed differences in these interactions between the terrestrial and aquatic environment are due to the effects of water as a non-resource variable as well as due to special adaptive characteristics of aquatic plants. Further we hypothesize that the aquatic plants adopt both competitive and allelopathic strategies under different conditions and in interactions with different plants.

The review highlights that our knowledge of both competition and allelopathy among aquatic plant communities is inadequate and fragmentary, and therefore, both extensive and intensive studies are required.

### Zusammenfassung

Dieser Artikel bespricht die über Studien zu Konkurrenz- und Allelopathieverhalten bei Wasserpflanzengesellschaften veröffentlichte Literatur. In einem breiten Überblick über die Gesellschaft werden auch die Studien zu Interaktionen zwischen Makrophyten und Mikrophyten, Makrophyten und Makro-invertebraten und Mikrobengemeinschaften erörtert. Die Rolle dieser Interaktionen in der Struktur und Dynamik von Lebensgemeinschaften im Wasser wird im Licht aktueller Hypothesen zum Thema Konkurrenz bei Legensgemeinschaften auf dem Land diskutiert. Das vorhandenen Daten lassen vermuten, daß sich Wasserpflanzen verschiedener Wachstumsformen in ihrem Reaktions- und Anpassungsverhalten hinsichtlich Konkurrenz und Allelopathie beträchtlich voneinander unterscheiden. Die mögliche

Anwendung dieser Interaktionen in der biologischen Schädlingskontrolle und der Landwirtschaft wird ebenfalls zusammengefaßt.

Es wird deutlich, daß die bei diessen Interaktionen zwischen einer Land- und einer Wassenumgebung beobachteten Unterschiede sowohl auf die Wirkungen von Wasser als einer Nicht-Ressourcen-Variablen ("non-resource variables") als auch auf das besondere Anpassungsverhalten von Wasserpflanzen zurückzuführen sind. Im weiteren stellen wir die Hypothese auf, daß Wasserpflanzen unter bestimmten Bedingungen und in ihren Interaktionen mit verschiedenen Pflanzen sowohl Kompetitive als auch allelopathische Strategien einsetzen.

Der Überblick hebt hervor, daß unsere Kenntnisse von Konkurrenz und Allelopathie bei Wasserpflanzen unvollständig und unzulänglich sind und darum sowohl extensive als auch intensive Studien erfordern.

## I. Introduction

The aquatic plants (macrophytes) and their communities have until recently been among the most neglected components in the ecological studies of aquatic ecosystems. They generally occupy the shallow fringes (littoral zones) of both lentic and lotic waterbodies though some may grow under more than 12 m deep water (Spence, 1982). However, because the majority of the world's waterbodies are shallow and their littoral zone dominates over the pelagic (low pelagic/littoral ratio), the macrophytes assume an important role in regulating the structure and functioning of the aquatic systems (Wetzel, 1983b, 1990). The bulk of published literature on aquatic plants is concerned with their general biology, physiology and environmental responses (Gessner, 1955, 1959; Hutchinson, 1975; Sculthorpe, 1967). There are also many studies on primary production, nutrient relations and decomposition of aquatic macrophytes (Hutchinson, 1975; Westlake, 1980). Several plants which exhibit prolific growth and readily colonize aquatic habitats have received particular attention (Gopal, 1987; Landolt, 1986; Landolt & Kandeler, 1987; Pieterse & Murphy, 1990).

The study of aquatic plant communities has, however, remained bogged down in the controversy over defining an aquatic plant (Hartog & Segal, 1964; Hutchinson, 1975) and been largely confined to the description of growth forms and their classification (Best, 1988; Hartog & Segal, 1964; Hartog & van der Velde, 1988; Hejny, 1960; Hogeweg & Brenkert-vanRiet, 1969; Hutchinson, 1975). There are few studies of the patterns in community structure and composition, and the methods of vegetation analysis and classification so commonly used in the study of terrestrial communities (Feoli & Orloci, 1991; Okland, 1990) have rarely been applied to aquatic macrophytic vegetation (Best, 1988). Similarly, the studies on the dynamics of aquatic plant communities have emphasized the zonation of growth forms along a hydrological gradient and the role of life history characteristics of different species populations (Clements, 1916; Hejny, 1971; Segal, 1968; Tüxen & Preising, 1942; Van der Valk, 1981, 1987).

The community is not merely an assemblage of species populations in a given area. Its structure, functioning and dynamics are governed by various kinds of positive, negative or indifferent interactions between the species, besides their interactions with the environment. There has been very little effort devoted to the study of these interactions and their role in regulating the organization and dynamics of aquatic plant communities.

Among various interactions, competition, apart from trophic relationships, is the most important. The significance of competition had been recognized by Malthus (1798) and Darwin (1859) in population growth and evolution respectively. Later, Clements (1904) recognized competition as a major process in the succession of communities. Since then, competition has been the subject of innumerable investigations and considerable discussion in ecology (Grace & Tilman, 1990; Keddy, 1989). In a recent survey conducted by the British Ecological Society, competition was ranked fifth among the fifty most important ecological concepts (Cherrett, 1989).

The most common form of competition is the "exploitative competition" that occurs between two organisms of the same or different species whenever a valuable resource such as space, food or nutrients and light, shared by them is in limited supply (Harper, 1977; Pianka, 1981). In contrast to this, another kind of competition, the "interference competition", involves active denial of access to a resource by one competitor to the other (Begon et al., 1986). Both kinds of competition have been extensively investigated in terrestrial environments. For an overview, see Law and Watkinson (1989).

In another form of competitive interaction, called allelopathy, one of the competing organisms produces chemical substances which on being released into the environment retard the growth of another species providing it with a competitive advantage against the latter. According to Rice (1967), the ability of plants to produce phytotoxic compounds may have evolved in some cases as a means to suppress or kill their neighbours and thus eliminate the competition for limited resources. Although it is indeed very difficult to distinguish allelopathy from competition in the field (Harper, 1961, 1964; Muller, 1969), and some have even questioned its role in species interactions (Harper, 1977), there exists a large amount of experimental data to demonstrate the occurrence of allelopathy among terrestrial plants and its role in a number of ecological processes (Rice, 1974, 1979, 1984; Putnam & Tang, 1986). It is only during the past few years that interest has grown in the studies of both competition and allelopathy in aquatic plant communities. Some of these studies have recently been summarized by Elakovich and Wooten (1989a,b), McCreary (1991) and Meteiko (1981).

In this article, we first review the state of our knowledge of competition and allelopathy and their role in the structure and dynamics of aquatic communities, and their possible application in biological control and agriculture. Next, we discuss briefly the relative importance of these interactions, and finally, make suggestions for further investigations.

Following Hartog and van der Velde (1988), we consider the community in its broader sense to include the microphytes (epiphytes and phytoplankton) and invertebrates associated with the macrophytes and discuss their competitive and/or allelochemic interactions as well insofar as they influence the macrophytic communities. We further recognize the fact that the aquatic ecosystems variously interact with their adjacent terrestrial systems particularly at their interface (Loucks, 1990) and that the allochthonous input of terrestrial plant litter constitutes a potential influence on the aquatic plant communities. Likewise, the oft-recommended use of aquatic plants as mulch or manure (Nat. Acad. Sci., 1976) may affect the terrestrial vegetation, particularly crop plants, if the macrophytes have allelopathic potential. Hence, the available studies on these interactions are also reviewed here. A conceptual framework for various interactions in aquatic macrophyte communities is given in Fig. 1.

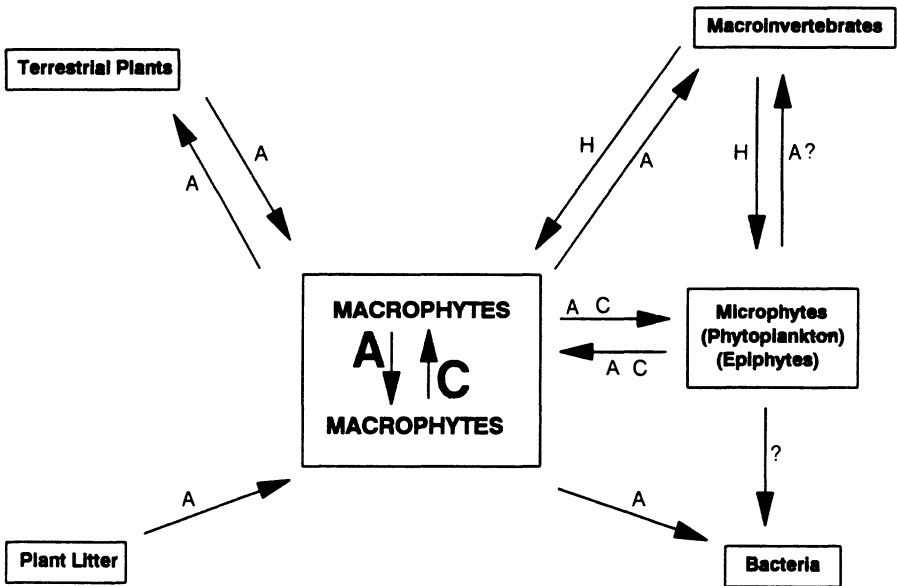


Fig. 1. Conceptual diagram of major interactions in aquatic plant communities. A = Allelopathy, C = Competition, H = Herbivory. Large letters indicate that these interactions are of greater significance.

## II. Competition

Macrophyte growth and distribution are regulated by a number of factors as light, temperature and nutrients (Chambers, 1987; Chambers & Kalff, 1987; Dale, 1986; Jupp & Spence, 1977; Moeller, 1978; Titus & Adams 1979) which determine the species dominance ultimately affecting the outcome of competition. Westlake (1981) provides evidence that good reduction in light may result in species composition to change. For example, in the chalk streams of south Britain, tree shaded sites become dominated by *Berula erecta* or *Callitriche* species whereas *Ranunculus* species are excluded. The thermal optimum for many submerged freshwater macrophytes appears to be in the range of 28 and 32 C (Barko & Smart, 1981). Therefore, the adaptability of submerged macrophytes to lower temperatures may confer a competitive advantage to some species. Similarly, better ability of some species to accumulate enough nutrients from a nutrient-poor environment enables them to dominate the area.

Based on the field observations of changes in the dominance of various macrophytes over time, several workers have speculated on the role of competition. Misra (1938) speculated that between species competition might affect the distribution of some aquatic plants. Zutshi and Vass (1976) reported that *Myriophyllum* species is able to outgrow *Hydrilla verticillata*, *Potamogeton lucens* and *Ceratophyllum demersum* in water culture because it forms adventitious roots from its cut ends within 12–20 hours which give it competitive advantage over other species in colonizing the area. The suppression of growth of the submerged macrophytes by floating leaved and free floating species like *Trapa bispinosa*, *Nelumbo nucifera*, *Nymphaea* spp., water

hyacinth and *Salvinia* which cut off light penetration totally, is also often interpreted as competition (Philipose et al., 1970; Ramaprabhu, 1972; Rai et al., 1980; Rai & Dattamunshi, 1981).

#### METHODOLOGY

Interspecific competition can be studied in several ways. The most common method is the manipulative experiment in which the total density of the mixture of two competing species is kept constant by altering the proportion of individuals of either species. This is referred to as the "replacement series" (DeWit, 1960). Several sets with different total density can also be used. The other common method is to grow the competing species in pure stands at different densities. In mixed culture, the number of one species is kept constant and the number of the other species varied. Species may be cultured at different densities and in different combinations. This is referred to as "additive" or "substitution series." In field studies also, it is possible to study competition by removing plants of one or more species in a community. The effect of thinning on the growth of the remaining species/individuals allows better evaluation of competition because other environmental factors remain nearly undisturbed. Experimental studies of competition in aquatic macrophyte communities are, however, uncommon and their conclusions vary according to the species and environmental variables considered (Wilson & Keddy, 1985a).

In aquatic environments, competition is expected to occur most between species of similar growth forms occupying identical position in the water column. Rooted submerged plants like *Vallisneria* species may not compete for nutrients or space with other submerged forms like species of *Ceratophyllum* and *Utricularia* or the free floating species. We therefore consider it desirable to discuss competition among plants of different growth forms separately. However, it may be pointed out that McLay (1974) has reported interference between emergent, submerged and free floating macrophytes without discussing competition. He observed that *Potamogeton pectinatus* was excluded by *Scirpus californicus* which also affected the growth of *Lemna perpusilla*. Both *Lemna* and *Potamogeton* species also affected each other.

#### FREE FLOATING MACROPHYTES

Various free floating macrophyte species differ greatly in their size and growth form. At one end of the spectrum lie the species of *Wolffia* with a tiny globose frond without roots that remains just on the water surface. On the other end lies water hyacinth which often develops more than one meter tall leaves above the water surface and also an extensive fibrous hairy root system hanging equally deep into the water. Under favourable conditions of nutrient supply and temperature, all free floating macrophytes keep multiplying vegetatively until they cover the entire surface of a waterbody and the space becomes a limiting factor. They often give the impression that the growth in such plants is density independent and that the growth of individuals within the population is not limited by space or nutrients.

Duckweeds (Lemnaceae) have been investigated in some detail, largely because of their small size, rapid growth and the ease with which they can be cultured on synthetic media under controlled conditions. In one of the earliest studies, no distinct effect of competition could be noticed in pure or mixed culture of *Spirodela punctata* and



*Lemna minor* (Ikusima, 1955; Ikusima et al., 1955). Landolt (1957) determined the growth rates of 12 species of duckweeds under a combination of several light, temperature and nutrient levels. On the basis of differences in the growth rate, he ranked the competitive ability of different species. He observed that in nature, the competition between duckweeds for space and light is decided by the rapid growth and the struggle for nutrients is decided by the ability of a species to utilize them from diluted solutions (Landolt, 1957). *Lemna trisulca* and the species of *Wolffiella* (*W. floridana* and *W. lingulata*) grow submerged and hence they do not compete for space. These species can also utilize nutrients in low concentrations and grow well under low light intensities (probably because they can utilize the carbohydrates secreted out into water by other Lemnaceae).

A growth analytical approach has been followed in several studies of competition in many lemnids and other free-floating species. Clatworthy and Harper (1962) studied three lemnids [*Lemna gibba*, *Lemna minor* and *Spirodela polyrhiza* (= *Lemna polyrhiza*)] and *Salvinia natans* under laboratory conditions in culture media. They observed that in monocultures, the relative growth rate of all the species declined with increase in density (self crowding) and hence, the shortage of nutrients. Further, the mean frond weight also declined in *Lemna minor* and *S. polyrhiza* but remained unaffected in *L. gibba*. Reddy and DeBusk (1985) also observed a similar linear fall in the specific growth rate with increasing density of *Lemna minor* (from 0.118–0.273 day<sup>-1</sup> at 30 g/m<sup>2</sup> to 0.01–0.05 day<sup>-1</sup> at 130 g/m<sup>2</sup>) and *Spirodela polyrhiza* (from 0.08–0.237 day<sup>-1</sup> at 20 g/m<sup>2</sup> to 0.002–0.01 day<sup>-1</sup> at 100 g/m<sup>2</sup>).

Studies on the growth of lemnids and *Salvinia natans* in mixed cultures (Clatworthy & Harper, 1962) showed that the total biomass yield of two species mixtures remained constant but wide variations occurred in the proportion of component species. These differences could not be explained by the differences in relative (intrinsic) growth rate, arithmetic growth rate and final yield of the species in monocultures. Whereas *Lemna minor* had the highest relative growth rate followed, in decreasing order, by *S. natans*, *L. gibba* and *S. polyrhiza*, it had the lowest arithmetic growth rate and the yield was lower than that of *S. polyrhiza* which had the maximum yield. In mixed cultures, *S. natans* and *L. gibba* had better performance than that of *L. minor* and *S. polyrhiza*. Clatworthy and Harper (1962) concluded that the morphological features such as the gibbosity of *L. gibba* and the persistent stem of *S. natans* determine the success during competition by helping the species to occupy the surface layer of a mat and overshadowing the fronds of other species. Rejmankova (1975) made similar observations both in the field and under laboratory conditions and confirmed that *L. gibba* has a competitive advantage over *L. minor* because the former can shade out the latter species due to its gibbosity.

In another study, Wolek (1974) observed that *Spirodela polyrhiza* was a better competitor than *Lemna gibba* and *Lemna minor*, and *Wolffia arrhiza* was the weakest. He concurred with Clatworthy and Harper (1962) that it is not possible to predict the success of a species in competition from the growth rate in pure cultures. The intrinsic growth rate of *Lemna minor* was observed to be lower than that of *Lemna gibba* but the mean growth rate was higher than that of *Wolffia arrhiza*, *Spirodela polyrhiza* and *L. gibba*. Wolek (1974), however, attributed the differences between species to the competition for nutrients, and observed that competition for mineral salts inhibits the growth rate of a weaker competitor in mixed cultures whereas the stronger species remains undisturbed. He further emphasized that the morphological characteristics



like longer roots or strongly developed underwater parts play a decisive role. One might assume that the same morphological features may express various competitive values depending upon particular conditions. Kaul and Bakaya (1976), studying competition between *Spirodela polyrhiza*, *Lemna minor* and *Lemna trisulca*, confirmed the results of Wolek (1974). They observed that the growth of individual species was better when grown alone than in mixture, and that *Spirodela* has competitive advantage over the other two species.

It is important to note that there are large differences between various strains of the lemnids (Landolt, 1986), and Wolek (1984) himself demonstrated differences in the competitive ability of different clones of *S. polyrhiza* in mixed cultures with *L. minor*. It is therefore likely that much of the difference in the results of various studies can be explained by the differences in the clones examined.

The competition for nitrogen and phosphorus in lemnids has also been demonstrated by Docauer (1983). He observed large differences in the growth rate of *Spirodela polyrhiza*, *Wolffia borealis* and *Lemna turionifera* grown in media with different N/P ratios (0.2, 2.7 and 150). In mixed cultures, the growth of *L. turionifera* was not affected by *W. borealis* but reduced by *S. polyrhiza*. On the other hand, *L. turionifera* lowered the growth of *W. borealis* drastically at low N/P ratios, and to a lesser extent also of *S. polyrrhiza* at both low and high N/P ratios.

Interspecific competition between *Lemna minor* (floating) and *Lemna trisulca* (submerged) has been investigated in some detail both in the laboratory and under field conditions. Bornkamm (1970) observed that *L. trisulca* was a weaker competitor. In mixed cultures, its dry matter and protein production declined from that in monoculture. Keddy (1976) obtained similar results but observed that *L. trisulca* was able to maintain a growth rate 70% of that in control when shaded by *L. minor* but the latter species did not tolerate shading. Further investigations by McIlraith et al. (1989) confirmed the competitive superiority of *L. minor* over *L. trisulca* because it floats at the surface and is shaped like an oblate spheroid. It is suggested that this shape coupled with horizontal orientation, efficiently intercepts light from any angle (Niklas & Kerchner, 1984). *Lemna trisulca* was, however, better suited for efficient nutrient uptake due to its submerged, thin and elongate fronds with a large surface area. *Lemna minor* intercepts light before submerged *L. trisulca* is able to use it (McIlraith et al., 1989). Thus, in a shaded eutrophic site, light limitation prevents *L. trisulca* from becoming dense enough to limit nutrient availability for *L. minor* which gains dominance. In a relatively unshaded, less eutrophic site, *L. minor* does not attenuate incident light appreciably and therefore, *L. trisulca* outcompetes it for nutrients and holds it at a low density. These differences also explain their co-existence under certain nutrient limited conditions.

Similarly great interest has been shown in the competitive ability of water hyacinth (*Eichhornia crassipes*), one of the world's worst aquatic weed (Gopal, 1987). Water hyacinth multiplies vegetatively very rapidly and forms dense mats. As the density increases the plants start vertical growth (elongation of petioles) together with an increase in leaf surface area. Center and Spencer (1981) have shown that both the leaf length and its diversity are greatest during the period of high density. They interpreted the inverse relationship between the density and size as a strategy in intraspecific competition and the increase in density and size as alternative forms of growth associated with the degree of competition.

Further, the suppression of flowering at low light intensities also allows more lateral

buds to develop into stolons. But the ramet production which is also contingent upon light penetration beyond the uppermost leaves, is not sustained under a dense high monolayered canopy (Center & Spencer, 1981). Hence, a reduction in plant density occurs by loss of younger plants as a self regulatory self-thinning mechanism.

Detailed studies on the growth of water hyacinth in Florida under nutrient non-limiting conditions (DeBusk et al., 1981; Reddy et al., 1983; Reddy & DeBusk, 1984) show that the specific growth rate (% increase per day) is maximum ( $0.06\text{--}0.07\text{ day}^{-1}$ ) at a low plant density (about  $400\text{ g/m}^2$ ) and decreases linearly with increase in density ( $0.001\text{ day}^{-1}$  at  $1900\text{ g/m}^2$ ). It is also interesting to note that the plants maintained a high growth rate ( $\text{g/m}^2/\text{day}$ ) throughout the year except for two winter months (Reddy & DeBusk, 1984).

The great morphological plasticity of the plant coupled with its wide ecological amplitude which allow a high growth rate over a long period, also provide water hyacinth a competitive advantage over other free floating macrophytes. Gay (1960) reported the disappearance of *Pistia stratiotes* from some regions of White Nile after invasion of waterhyacinth. Little (1966) also observed waterhyacinth to compete with and replace *Pistia stratiotes* in Lake Apanas (Nicaragua). He ascribed this to the development of large leaf canopy which shaded out smaller *Pistia* plants. In a recent experimental study, Agami and Reddy (1990) also concluded that the luxuriant growth and high plasticity of *Eichhornia* plants enabled them to grow above the *Pistia* plants, thus shading and stressing them. In an earlier report, Parija (1934) observed that *Pistia* had a lower growth rate than water hyacinth, and in the long run water hyacinth kills *Pistia*.

Chadwick and Obeid (1966) observed that the competitive advantage of water hyacinth over *Pistia* is related to the pH optima for their maximum growth. Whereas water hyacinth had a pH optimum near 7 for both increase in dry weight and number of plants, *Pistia* had its maximum growth at pH = 4. In *Pistia* the increase in dry weight is largely due to increased growth of individuals but in water hyacinth there is a greater increase in the number of plants. *Pistia* has also a narrower range of tolerance to variations in pH than that of water hyacinth. Thus, in most of the field conditions suitable for water hyacinth, pH limits the growth of *Pistia*. Further, the ability of water hyacinth to modify pH near its optimum requirement (Abu Gideiri & Yousif, 1974; Parija, 1934) also appears to be an important factor.

Tag el Seed (1978) studied competition with *Pistia stratiotes* in mixed culture using replacement series (keeping the density constant). Water hyacinth displaced *Pistia* at all pH levels despite the fact that at pH = 4 *Pistia* had the optimum growth. He also observed greater increase in biomass and number of plants of water hyacinth in mixed culture than that of *Pistia*. However, the results appear to have been influenced by the very small size of the containers.

Another free floating competitor of water hyacinth is *Salvinia*, particularly *S. molesta* in the tropics. In the waterways of Kerala (India) water hyacinth commonly occurs with *Salvinia molesta* which often appears to exclude water hyacinth. Sudds composed of two species are also frequently seen in shallow water bodies. We have also observed *Salvinia molesta* to take over and exclude water hyacinth in a waterbody near Delhi. Under experimental conditions, DeSilva et al. (1984) observed that in mono-cultures water hyacinth grew exponentially from the beginning but *Salvinia* had a lag phase. When grown together in 1:1 ratio, water hyacinth had the advantage in the beginning but as the growth of *Salvinia* entered the exponential phase, *Salvinia*

took over and the differences in the growth of the two species were reduced to small values. Recently, Singh (1992) has observed that *Salvinia molesta* competes successfully with *Azolla pinnata* and *Spirodela polyrhiza* whose growth is significantly reduced in mixed culture with *Salvinia*.

Like water hyacinth, *Salvinia molesta* and *Pistia stratiotes* also exhibit morphological plasticity in growth under crowded conditions as the leaves grow larger, and more vertically oriented. The stems of *Salvinia molesta* are fragile and the ramets readily drift apart if space is available. Harper (1977) noted that *Salvinia molesta* continues to grow at the intrinsic rate until the whole surface of a waterbody has been covered, and that the crowded plants grow slower than uncrowded plants because they contain less nitrogen due to root competition. In both *Pistia stratiotes* and *Salvinia rotundifolia*, however, the specific growth rate has been observed to decrease linearly with increasing density (Reddy & DeBusk, 1984, 1985; Tucker, 1983).

Pennywort (*Hydrocotyle umbellata*) offers an interesting case of competition with water hyacinth. Both the species coexist throughout the year in many areas of Florida. The growth of water hyacinth is severely affected by frost during the winter whereas *H. umbellata* tends to flourish during the cold period (Clough et al., 1987; Reddy, 1988; Reddy & Debusk 1984). After a frost, *E. crassipes* plants recover by growing new shoots and ramets after a few weeks, and then during the summer they impose severe stress on *H. umbellata* because of their relatively higher growth rate (Reddy & Debusk, 1984). An experimental study showed that *H. umbellata* grew better in mixed cultures with water hyacinth than in monoculture (Agami & Reddy, 1990). The petioles of *Hydrocotyle* leaves in mixed cultures elongated to such a height that they were not affected by the luxuriant growth of *Eichhornia*. A field study further confirmed that in mixed cultures with water hyacinth, *H. umbellata* produced more biomass than plants grown in monoculture though the root:shoot ratios of both the species declined (Agami & Reddy, 1991). It is also interesting to note that the specific growth rate of pennywort increases with density upto a certain level (about 500 g/m<sup>2</sup>) before declining at high densities (Reddy & DeBusk, 1984).

In another study of interspecific competition, Agami and Reddy (1989) examined the biomass and nutrient accumulation of *Salvinia rotundifolia* and *Spirodela polyrhiza* in mono- and mixed cultures. In mixed cultures of equal density the growth rate of *Salvinia* was higher and it produced two times more biomass than *Spirodela*. The standing crop of *Salvinia* was not affected by the presence of *Spirodela* which accumulated about 15 times more nitrogen and phosphorus than *Salvinia* in mixed cultures whereas in monocultures the uptake of nutrients was similar in both the species.

#### SUBMERGED MACROPHYTES

Most of the submerged macrophytes form dense stands, but the effects of density (intraspecific competition) have rarely been examined. In recent years, interspecific competition has however been investigated in some detail (see review by McCreary, 1991).

The submerged macrophytes exhibit two major types of growth forms. Some like charophytes, *Isoetes*, *Vallisneria*, and submersed species of *Eleocharis* are stoloniferous and form rosettes with limited height of shoots or leaves. The other macrophytes whether rooted (like *Hydrilla verticillata*, *Myriophyllum spicatum*, *Najas graminea*,

*Zannichelia palustris*, *Potamogeton pectinatus*, etc.) or not (e.g. *Ceratophyllum demersum* and *Utricularia* species) tend to develop long shoots and branch out near the water surface forming a canopy (Spencer & Lekic, 1974). Whereas the rosette forming species may face competition for space at high densities, the canopy forming species can attain a much higher density before the competition for space sets in. Sutton et al. (1980) observed no ill effect of high density in *Hydrilla verticillata* on growth or vegetative propagation as they recorded as many as 4000 turions/m<sup>2</sup> in a dense stand. The rosette forming species are also differentiated into two groups according to their growth strategies (McCreary, 1985; McCreary & Carpenter, 1987): (a) species which maximize on horizontal space by developing numerous and/or distantly placed ramets (guerilla strategy; see Lovett-Doust, 1981; Lovett-Doust & Lovett-Doust, 1982) and (b) species which produce fewer, closely placed and larger ramets (phalanx strategy).

The interspecific competition has been examined between species of both similar and different growth forms and growth strategies, and both in the field and laboratory conditions. Moen and Cohen (1989) examined both intra- and interspecific competition in two canopy forming species, *Potamogeton pectinatus* and *Myriophyllum exalbescentis* in aquaria at low and high densities. The growth rate decreased with increasing plant density in both the species but whereas the higher density resulted in smaller roots, shoots and tubers in *P. pectinatus*, in *M. exalbescentis* only the shoot biomass was adversely affected. They further observed that the *P. pectinatus* takes the initiative of growing earlier than *M. exalbescentis* and outcompetes it. In mixed cultures, besides having a higher initial growth rate, *P. pectinatus* also grows near the water surface and shades the leaves of *M. exalbescentis* which exert no competitive effect on the former (Moen & Cohen, 1989).

*Myriophyllum spicatum* is a better competitor than *Vallisneria americana* but the two species coexist in the littoral zones of lakes of Madison (Wisconsin) due to differences in their adaptations to low light intensity (Titus & Adams, 1979). *Myriophyllum spicatum* is able to adapt to low light availability via leaf sloughing and plasticity in growth form. In contrast, *Vallisneria americana* has more efficient carbon fixation at low light. The two species also exhibit both temporal and spatial partitioning of the habitat. *Vallisneria* is a summer specialist whereas *Myriophyllum* grows better in winters. *Vallisneria* occurs at greater water depth and *Myriophyllum* occurs in shallow waters. Recently, Madsen et al. (1991) have also observed that *Myriophyllum* suppresses the growth of other submerged macrophytes.

Titus and Stephens (1983) demonstrated that *Vallisneria americana* responds to competition from other species by producing longer leaves at the expense of vegetative multiplication and horizontal spread. A field study, at three different sites dominated by *Potamogeton amplifolius*, *Chara vulgaris* or *V. americana* within the lake Chenango (New York), showed significant differences in the growth of *Vallisneria americana* at the three sites. Plant dry weight, mean leaf length, number of rosettes per plant, stolon length, number and weight of winter buds were lowest at the *Potamogeton amplifolius* dominated site and maximum in its own stand. They observed that the removal of neighbours, early in the growth period, resulted in shorter leaves but more rosettes per plant of *V. americana* at all the three sites. Plant dry weight was consistently but not significantly higher in the absence of neighbours. The increased leaf length has been interpreted as a response to shading by adjacent plants, and the increase in number of rosettes as a response to open habitat (Titus & Stephens, 1983).

Several studies have shown that *Hydrilla verticillata* is a strong competitor than other submersed species like *Vallisneria neotropicalis* (Haller & Sutton, 1975). *H. verticillata* not only forms a dense canopy at the water surface which reduces light penetration by at least 95% but has several other biological and physiological attributes that contribute to its success. *Hydrilla* invests relatively little in its roots (low root tissue to foliage ratio) but profusely in vegetative propagation (numerous tubers and turions). *Hydrilla* also has a lower chlorophyll a:b ratio than that in terrestrial plants (Haller, 1974) and this may enable the plant to use more effectively the shorter wavelengths of light for photosynthesis. *Hydrilla* also replaces native submersed species such as *Ceratophyllum*. Van et al. (1976) attributed this to a low light requirement of *Hydrilla* to achieve the maximum photosynthetic rate and its ability to utilize carbon dioxide early in the morning when the supply is high thereby reducing its availability to other plants during the day. Steward (1988) has however shown that the success in competition between *H. verticillata* and *V. spiralis* is related to the fertility of the water. The effect of water chemistry on competition among submerged macrophytes has also been demonstrated by Smart and Barko (1989). It is also interesting that floating leaved species like *Nelumbo lutea* can suppress *Hydrilla* by developing a dense leaf cover on the water surface and almost totally eliminating light penetration (Johnston et al., 1983).

Schloesser et al. (1985) studied the seasonal changes in submersed macrophyte communities at Stag, Russell and Sugar Islands in a major river system. They observed that at both Stag and Russell Islands, the decline of narrow leaf forms of *Potamogeton* sp. was associated with simultaneous increase of *P. richardsonii*. At Russell Island, during summer *Elodea canadensis* replaced *P. richardsonii* by September, and later during winter, *Elodea* was replaced by *Myriophyllum spicatum*. They inferred that *P. richardsonii* competed successfully with the narrow leaved species of the genus and that the decline of *M. spicatum* between August and October at Sugar Island was probably a result of competition with *Heteranthera dubia* because *M. spicatum* did not decline where *H. dubia* was lacking.

The competitive ability of some *Potamogeton* species has been investigated in several recent studies. Kautsky (1991) examined the interactions between three species of *Potamogeton* (*P. pectinatus*, *P. filiformis* and *P. perfoliatus*), *Ranunculus baudotii*, *Ruppia cirrhosa* and *Zannichelia* sp. in reciprocal replacement series experiments. *P. pectinatus* was unaffected by the presence of *P. filiformis* but was significantly suppressed by *P. perfoliatus*. However, when *P. pectinatus* was grown with *Ranunculus baudotii* or *Ruppia cirrhosa*, both species in the mixture suppressed each other. Observations on three combinations of two species (*P. pectinatus* and *Zannichelia palustris*, *P. filiformis* and *Z. palustris*, and *P. filiformis* and *P. perfoliatus*) showed that interspecific relationships were generally weaker than intraspecific. In another study of interactions between *P. pectinatus* and *P. gramineus*, Spencer and van Vierssen (1988) observed that the light regime governed the outcome of competition as *P. gramineus* required less light than *P. pectinatus*. It has also been observed that *P. pectinatus* could outcompete *P. gramineus* if both the species are raised from large sized tubers but *P. gramineus* was the successful competitor when the plants were raised from average sized tubers (Spencer, 1988). McCreary (1991) suggests that the larger tubers may provide additional nutrients and that "a nutritional advantage can be quickly translated into a light advantage" under low light regimes. However, why *P. gramineus* is unable to take advantage of larger tubers is not clear. It is



important to note that large variations exist between different populations of *P. pectinatus* (Pip, 1984, 1987) and it is likely that these populations differ also in their competitive ability.

In an interesting in situ study of competition using species removal method, Chambers and Prepas (1990) observed that the distribution and biomass of submerged species like *Myriophyllum exalbescens*, *Ceratophyllum demersum* and *Chara* sp. were not affected by competition and that the abiotic factors and spatial heterogeneity were more important factors.

An interesting example of competitive interactions among rosette forming species is that of *Eleocharis acicularis*. It grows under a wide range of light and temperature conditions in a variety of shallow water habitats which also differ in their water chemistry (Hutchinson, 1975; Yan et al., 1985). It often grows with *Juncus pelocarpus* forma *submersus*, another rosette forming species of similar habit (Swindale & Curtis, 1957). Competition between the two species has been studied in situ using multiple density reciprocal replacement series at two different light regimes (McCreary, 1985; McCreary et al., 1983). The growth (in terms of biomass yield) of both the species is adversely affected by higher density and shading but the effect of low light intensity is much less than that of density. Yet, in mixtures, there appeared to be no competition between the two species at any of the density or light levels. The nature of the substrate also did not exert any influence (McCreary & Carpenter, 1983, 1987; McCreary et al., 1983). It was concluded that "the two species are non-randomly intermingled and capable of stable coexistence under a variety of different environmental conditions." Though no explanation could be found for coexistence in nature, environmental variation was expected to outweigh interspecific interference in determining abundance of the two species in natural associations (McCreary et al., 1983). Recently *Eleocharis acicularis* has been shown to have C<sub>4</sub> acid fixation and high photosynthetic rate at low irradiance levels depending upon free carbon dioxide (Morton & Keeley, 1990). The coexistence of *E. acicularis* with *Juncus pelocarpus* f. *submersus* may also be explained by the possibility of a different photosynthetic pathway in the latter species. This is indicated by its co-occurrence with *Isoetes howellii* which is known to be a CAM plant (Keeley, 1981).

Another study of competition between *Eleocharis acicularis* and *Eleocharis coloradoensis* demonstrated that *E. acicularis* tolerates and grows better at lower light and lower temperature conditions whereas *E. coloradoensis* has better growth under more light and higher temperature regime (Ashton & Bissell, 1987). *Eleocharis acicularis* gets established earlier than the other species when the water temperature is still low and was therefore a better competitor.

However, *Eleocharis coloradoensis* has been reported to displace several submerged aquatic macrophytes such as *Potamogeton pectinatus*, *P. nodosus*, *P. pusillus*, *P. crispus*, *Najas guadalupensis*, *Elodea canadensis* and *E. nutallii* in many habitats (Ashton et al., 1985; Frank & Dechoretz, 1980; Yeo, 1980; Yeo & Fisher, 1970; Yeo & Thurston, 1984). In laboratory experiments, *Eleocharis coloradoensis* reduced significantly the number of shoots of *Potamogeton nodosus* and reduced the production of subterranean turions of *Hydrilla* and tubers of *Potamogeton* by more than 50%. Different aquatic weeds, however, differed in their susceptibility. Based on the effect on dry weight, they were (in decreasing order): *Zannichelia palustris*, *Elodea nutallii*, *Elodea canadensis*, *Hydrilla verticillata*, *Potamogeton nodosus*, *Potamogeton pectinatus* and *Myriophyllum spicatum*. Recent studies have provided evidence that

the interaction of *E. coloradoensis* with other macrophytes is allelopathic in nature (see page 173).

#### EMERGENTS

There is very little information on the effect of density among emergent macrophytes. In *Phragmites australis* (= *P. communis*) which has been widely investigated in Europe, the relationship between shoot density and shoot biomass has been examined in several cases with a view to estimate aboveground production (Bjorndahl, 1983; Graneli, 1987; Mook & van der Toorn, 1982). These studies show that the shoot weight declines with increasing shoot density in accordance with the  $-3/2$  power law (cf. Yoda et al., 1963) during the early stages of growth. In *Typha angustata* also, the shoot length, shoot weight and leaf size decrease with increasing density under space-limited conditions (B. Gopal, pers. observ.).

In one of the earliest studies of interspecific competition, Buttery and Lambert (1965) analyzed the interactions between *Glyceria maxima* and *Phragmites australis* (= *P. communis*) in an area of primary fen. *Glyceria* starts growth early in the year but *Phragmites* becomes dominant in the later stages of succession. Both species reproduce vegetatively to form virtually monospecific stands. *Glyceria* has a short lived shallow rhizome which produces a series of new shoots throughout the growing season. The rhizomes of *Phragmites* are persistent and deep seated and the whole annual complement of aerial shoots emerges in late spring. Both species exhibit a reduction of growth from front to back of the fen. Buttery and Lambert (1965) concluded that *Phragmites* succeeds in competition probably due to its better tolerance of unfavourable substrate conditions and the differences in seasonal growth behaviour of the two species.

Szczepanska (1977a) observed that in mixed cultures, the reed (*Phragmites australis*) was constantly pushed out by the sedge (*Carex hudsonii*). The biomass of *Carex* in mixed cultures was almost twice higher than that in monocultures. In another study, *Typha latifolia* was found to compete successfully with *Phragmites australis*. In mixed cultures, *Typha latifolia* gained biomass whereas *Phragmites australis* (= *P. communis*) lost (Szczepanska & Szczepanski, 1982). Similar reduction also occurred in other growth parameters (growth rate, shoot-height, weight and number) of *P. australis*.

In another study concerned with the competitive ability of *Phragmites australis*, Yamasaki (1990) concluded that the dominance of *Miscanthus sacchariflorus* in the moist upper shoreline is due to the delayed emergence of *P. australis* during the post-flood growth phase.

In a study of competition between *Typha latifolia* and *T. angustifolia*, Grace and Wetzel (1981) demonstrated that morphology and water depth determine the success of the species. In shallow water, *T. latifolia* is competitively superior and can displace *T. angustifolia* which is better able to grow in deep water. The two species co-occur in marshes and ponds in the midwestern United States but are segregated according to water depth with *T. latifolia* in shallow water and *T. angustifolia* in deeper water. Grace and Wetzel (1981) observed that the two species coexist due to a deep water refuge for the competitively inferior *T. angustifolia* with thinner, taller leaves and fewer larger rhizomes. *T. latifolia* is prevented from growing in deep water because of the higher cost of producing broader leaves but it is better able to compete for light in shallow water because of its greater leaf surface area.



Grace (1987) reported that the relative competitive abilities of *Typha latifolia* and *Typha domingensis* were size dependent. When *Typha latifolia* and *Typha domingensis* were started from seeds, the results of competition favoured *Typha domingensis* especially at higher densities and in deeper water. *Typha domingensis* was clearly the superior competitor, when the two species were given equal status. On the other hand, when *Typha latifolia* and *Typha domingensis* were started from transplants and allowed to compete as adults, *Typha latifolia* was consistently the better competitor at all depths and its advantage increased over time. Pre-emption had a strong effect on early growth and distribution of the species. After the initial effects of temporal disadvantage, delayed plants were able to recover under certain circumstances. Both species recovered better in shallow water than in deep water. *Typha latifolia* recovered better than *Typha domingensis*. If both species survive the initial phase of competition and the habitat remains undisturbed, subsequent vegetative spread and competitive displacement can overcome the initial effects of spatial and temporal pre-emption resulting in a predictable zonation.

Similar observations have been made on competition between two Indian species of *Typha*, *T. angustata* and *T. elephantina* (B. Gopal, unpublished; Singh, 1992). Both form extensive monospecific stands but may occur together. *T. elephantina* differs from *T. angustata* in its deep seated extensive rhizome system (Sharma & Gopal, 1980). Whereas *T. elephantina* is able to grow (though reduced in size and does not flower) in upland areas which are subjected to only short term flooding, *T. angustata* does not tolerate drying of substrates for long. Further, the field observations show that *T. angustata* rhizomes tend to creep towards water but those of *T. elephantina* grow away from the water. The established stands of *T. elephantina* tolerate permanent deep flooding though the growth is slightly reduced. The best growth of *T. angustata* on the other hand is obtained in 10–15 cm deep water, and greater water depth for longer periods has an adverse effect (Singh, 1992). The competition and coexistence of the two species is therefore determined by the timing and duration of flooding which affect the establishment of the stand. *T. angustata* establishes itself readily from seeds on waterlogged soils and subsequent flooding accelerates its growth. Though the seeds of *T. elephantina* germinate in nature, they fail to give rise to a stand for hitherto unknown factors. In mixed culture, *T. angustata* grows better under waterlogged condition whereas at field capacity, *T. elephantina* has the advantage (Singh, 1992).

Similarly, *Phragmites karka* commonly occurs both in water and on moist soils but in association with *T. elephantina* or *T. angustata*, it grows usually on less waterlogged fringes. An experimental study showed that under waterlogged conditions, the growth of *P. karka* is reduced but at field capacity, the *Typha* species are adversely affected (Singh, 1992).

Sharma and Pradhan (1983) reported, on the basis of field observations, intense competition between *Typha angustata* and *Polygonum glabrum*. They noted that the standing crop of *Typha* was very much reduced (793 g/m<sup>2</sup>) in the *Polygonum* stand as compared to that in a nearby pure stand (8132 g/m<sup>2</sup>). Experimental studies have confirmed that in mixed cultures, *Polygonum glabrum* adversely affects the growth of *Typha angustata*, *T. elephantina* as well as *Phragmites karka* (Singh, 1992).

Another study demonstrated competition between *Brachiaria mutica* and *Typha angustata* with the former replacing the latter species within 10–12 months of planting in the stand (Mehta & Sharma, 1975).

Pawlowski and Zarzyski (1972) and Jasnowski (1975) observed that during succes-

sion the sedge *Carex* pushes out the rushes. They pointed out that as the water becomes shallower, sedge communities appear and develop in the rushes posing threat for the already established rush communities. Thus, the environmental changes were responsible for succession.

Interspecific competition has been recently demonstrated between six species of wetland plants (*Cyperus rivularis*, *Eleocharis obtusa*, *Juncus salicaria* (all obligate annuals), *Lythrus salicaria*, *Mimulus ringens* and *Verbena hastata* (all facultative annuals) by Johansson and Keddy (1991) who observed that the yield of the species in mixtures in most cases was significantly lower than in monoculture. *Lythrum*, *Cyperus* and *Juncus* had a stronger suppressive ability and were better competitors than *Eleocharis*, *Mimulus* and *Verbena*. It was concluded that the intensity of competition increased with increasing similarity between interacting plants as predicted by the niche control paradigm, and the asymmetry of competition decreased with increasing similarity as predicted by the dominance control paradigm (Johansson & Keddy, 1991).

Hutchinson (1975) and Spence (1982) have emphasized the importance of interspecific competition in producing shoreline zonation. Wilson and Keddy (1986b) examined competition among several shoreline species to explain their distribution along a gradient of exposure to wave action. They observe that this gradient incorporates both disturbance (through the removal of plant biomass) and stress (through the creation of a gradient in sediment organic matter, nutrient concentration and fine particle sizes). Various species differed significantly in their competitive ability measured as the relative increase in dry matter per plant in 1:1 species mixture under field conditions. The competitive ability was significantly correlated with mean position of the species on the exposure gradient (Wilson & Keddy, 1986b). *Eriocaulon septangulare*, a species of exposed shores with low organic matter content of sediments, had the lowest competitive ability whereas *Dulichium arundinaceum*, a species most common on sheltered shores had the highest competitive ability. Species like *Juncus pelocarpus* and *Rhynchospora fusca* were intermediate in nature. However, in another report, Wilson and Keddy (1985a) concluded that the distribution of *Juncus pelocarpus* on exposed shores was not determined primarily by interspecific competition. Though under experimental conditions, *Juncus pelocarpus* had better growth (a physiological response) at higher organic matter content of the sediments (Wilson & Keddy 1985b), its maximum biomass was obtained in exposed areas in field experiments (its ecological response; Wilson & Keddy, 1985a). They interpreted that the difference was due to additional factors in the field.

The relationship between diffuse competition and standing crop varied with the species: *Lysimachia terrestris* showed no correlation between diffuse competition and standing crop. *Juncus pelocarpus* showed a weak correlation and *Rhynchospora fusca* showed a strong correlation. Diffuse competition was most intense in relatively undisturbed habitats with high nutrient concentrations in the soil and relatively low on sandy shorelines, exposed to wave action and having nutrient poor soils.

Among several aquatic crops, rice is the most important and widely cultivated. A variety of aquatic plants are considered as weeds in paddy fields as they compete for nutrients and considerably lower its growth and yield. Misra et al. (1976) reported that *Chara* species cause considerable loss of yield because the plants become stunted and show poor tillering. *Ludwigia parviflora*, *Cyperus difformis* and several other species of *Cyperus* have been observed to adversely affect paddy yield (George, 1976). The

extensive root system and subterranean rhizomes of *Cyperus* species offer considerable advantage in competition with rice. Experimental studies are however few. Dey (1982) studied competition in detail between *Echinochloa crusgalli* and two cultivars of paddy, Pusa 2-21 and IR-8. The weed causes greater mortality in Pusa 2-21 while in IR-8 it adversely affects the tiller number, leaf area, shoot yield, flowering and seed weight.

#### WOODY WETLAND PLANTS

There are many woody plants of aquatic habitats but competition among them has not been studied except for a brief report on the competitive ability of *Melaleuca quinquenervia* which has invaded the *Taxodium distichum* swamps in Florida in the recent past. The success of *Melaleuca* has been related to the differences in its phenological and physiological attributes with those of *Taxodium* (Myers, 1984). It is observed that the "tolerance of both seeds and seedlings to submergence gives *Melaleuca* a competitive advantage over other woody species that can neither germinate under water nor tolerate submergence as seed or seedling." Thus, after a dry period followed by fire, immediately preceding the wet season, *Melaleuca* gets established well before *Taxodium* produces seeds in late fall season (Myers, 1984).

### III. Allelopathic Interactions

#### METHODOLOGY

Two distinct approaches have been used in the studies to demonstrate allelochemic interactions between different aquatic macrophytes and other organisms. In the first approach, growth of the interacting species is studied in the field or laboratory by manipulating the conditions so that the effects of competition are excluded. Kulshreshtha and Gopal (1983) grew the two submerged macrophytes in the same tank by placing them in two compartments separated by a wire mesh. In this situation, the plants do not interfere with each other directly and therefore, only the chemical substances released into the medium can be expected to influence the growth. The addition of individuals of an allelopathic species to an established stand of the other species may also result in suppression of growth of the latter. If this occurs in nutrient non-limited conditions and the introduced allelopathic species is also different in growth form, the logical conclusion would be in favour of allelopathic influence. Fuerst and Putnam (1983) have discussed these methodological aspects and the segregation of competitive and allelopathic interactions.

The other approach more widely used in recent years is that of bioassay (Leather & Einhellig, 1988) involving two different target species, terrestrial *Lactuca sativa* (lettuce) and aquatic *Lemna minor* (duckweed). Lettuce seeds are used to examine the inhibitory or stimulatory effects of an aqueous extract of the test plant on seed germination and seedling growth under controlled light and temperature conditions (Cheng and Reimer, 1988; Elakovich & Wooten, 1989a,b; El-Ghazal & Reimer, 1986; McNaughton, 1968; Sutton & Portier, 1989). Aqueous extracts are prepared by grinding the plant or plant parts in distilled water and the filtered extract is used as such or autoclaved. In many studies, the leachates prepared by soaking the test plant or test material in distilled water for different duration, have also been used.

A terrestrial plant may however not be a true indicator of the interactions involved in aquatic plants. Einhellig et al. (1985) also noted that bioassays are necessary tools in studying allelopathy and the choice of bioassay often dictates the interpretation of data. They also noted the lack of appropriate bioassays to detect inhibitory or growth regulatory compounds in leachates or extracts of aquatic species, and suggested the use of duckweed (*Lemna minor*) as a suitable target species (Einhellig et al., 1985). Several studies have shown that duckweeds are very sensitive to allelochemical phytotoxicity which can be measured readily in terms of a number of physiological and growth parameters including photosynthesis, respiration, chlorophyll and anthocyanin contents, biomass increase, flowering and vegetative multiplication (Cleland & Tanaka, 1982; Nyberg, 1986; Ramirez-Toro et al., 1988; Scholes, 1987). Rapid vegetative multiplication of duckweeds ensures that uniform material in sufficient amounts required for the bioassay can be readily obtained by growing the plant in a culture medium in controlled conditions. The cultured fronds are grown in small wells in an agar plate to which the allelochemic substance has already been added during the preparation of agar medium. It is reported that the duckweed bioassay can reliably detect the herbicide action or minute quantities of many allelochemicals (Leather & Einhellig, 1985, 1986, 1988).

Similar bioassays can also be performed on other plants in larger aquaria simulating near natural conditions to study the responses over a long period of time (Kulshreshtha & Gopal, 1983).

Besides testing the extracts or leachates, water samples taken from the waterbodies inhabited by plants suspected to be allelopathic have also been used in bioassay as the allelochemicals released by the plants are expected to accumulate to some extent in water bodies (Dooris & Martin, 1985; Szczepanska, 1987).

Anderson (1985) has developed another sensitive bioassays using explants of *Hydrilla verticillata* and vegetative propagules of *Potamogeton nodosus* and *P. pectinatus*. Martin and Martin (1988) used a commercially available apparatus Ecologen to culture *Hydrilla* and for studying the effect of allelochemicals released by the organisms or extracted from sediments. Several problems are evident in using bioassays. The mode of action of numerous potential allelochemicals may not be the same and often there is only a limited amount of sample available for testing. There is no perfect assay that will meet all the requirements for detecting the phytotoxicity of naturally occurring compounds and it would be prudent to use several for each case of suspected allelopathic interaction.

#### ALLELOPATHY AMONG MACROPHYTES

In one of the first reports of allelopathy among aquatic plants, Oborn et al. (1954) observed that under greenhouse conditions, *Potamogeton* species were eliminated from cultures in which it was grown with *Eleocharis acicularis* or with *Sagittaria subulata*. Since *Eleocharis* and *Sagittaria* produce shoots only a few centimeters in height as compared to the *Potamogeton* which may grow 2 to 4 m, competition for light was not considered to be responsible for the poor growth of *Potamogeton*. Since then several species of *Eleocharis* have been shown to have allelopathic properties against many other macrophytes.

Yeo (1980) reported that *Eleocharis coloradoensis* excludes or displaces several rooted submersed plants like *Potamogeton nodosus*, *Potamogeton foliosus*, and *Najas*

*guadalupensis* although some small plants like *Marsilea mucronata*, *Tillaea aquatica* and *Limnosella acaulis* were not displaced. It was suspected that *E. coloradoensis* may release an inhibitor specific for rooted submersed plants, but it was not detected in laboratory bioassays. Frank and Dechoretz (1980) also observed that the leachates from containers having cultures of *Eleocharis coloradoensis*, reduced the production of new shoots of *Potamogeton nodosus* and *P. pectinatus* and that the latter species was more sensitive of the two. Later, Yeo and Thurston (1984) reported the presence of inhibitor in dormant seeds of *Eleocharis coloradoensis*. Ashton et al. (1985) extracted a compound from the leachates of *Eleocharis* which was toxic to *Potamogeton pectinatus* and *Hydrilla verticillata*. They showed that very small pieces of *Eleocharis* by natural selection incorporate allelopathy among its mechanisms of competition.

Aqueous extracts from dried shoots of *Eleocharis interstincta* and *E. cellulosa* have been found to retard the growth of *Lemna paucicostata* (Sutton & Portier, 1989) and *Hydrilla* (Sutton & Portier, 1991). In *Hydrilla*, the number and weight of tubers was greatly reduced after 16 weeks growth. Only one gram of dry shoots of *E. cellulosa* caused 29% reduction in N content of *Hydrilla* shoots whereas 230 grams of *E. interstincta* could cause only 38% reduction in N content (Sutton & Portier, 1991).

Wooten and Elakovich (1991) tested the allelopathic potential of seven species of *Eleocharis*: *E. acicularis*, *E. equisetoides*, *E. flavescens*, *E. montana*, *E. obtusa*, *E. quadrangulata* and *E. tuberculosa* using lettuce and *Lemna minor* bioassay systems. All the species affected growth of lettuce seedlings at higher concentrations (125–250 ppt). *E. montana* and *E. tuberculosa* were most inhibitory even at lowest concentration (25 ppt) used in the study. *Lemna minor* bioassay was not that sensitive and no clear trend emerged.

Another species of *Eleocharis*, *E. geniculata*, and two species of *Sagittaria* (*S. graminea* and *S. subulata*) have also been shown to reduce the growth of *Hydrilla verticillata* when grown together (Sutton, 1986a, 1990). Shoot and root weight as well as number of tubers were all reduced by *S. graminea* to a greater extent than by *Eleocharis geniculata*. *Hydrilla* shoot weight was reduced by 90% and number of tubers by 59% in the presence of *Sagittaria subulata* (Sutton, 1990). These interactions have also been interpreted to be allelopathic in nature, and will be discussed later.

Dooris and Martin (1981, 1985) observed that *Hydrilla* does not thrive well in some lakes owing to the presence of natural products that may be derived from cypress (*Taxodium distichum*). The inhibitory material extracted from lake sediments is yet to be characterized. Sutton (1986b) examined the influence of several allelopathic chemicals on sprouting of *Hydrilla* tubers. Salicylic acid had the maximum potential to inhibit the sprouting of *Hydrilla* tubers and subsequent growth of the shoots. Martin and Martin (1988) also examined the influence of substituted phenols on the growth of *Hydrilla* at a very low concentration. They found that this concentration of all phenols was not as effective for inhibiting growth of *Hydrilla* as the naturally occurring inhibitor in lake sediments. The inhibitor from *Hydrilla* suppressed photosynthesis and increased the rate of respiration (G.M. Dooris et al., 1988). The chloroplasts from leaves of *Hydrilla* treated with inhibitor accumulated starch not observed in control plants. After four days of incubation, the chloroplasts of inhibitor treated leaves were markedly distorted. The amount of starch normally stored in leaves may be controlled by a partition of photosynthate between starch and sucrose. It appears that the *Hydrilla* growth inhibitor may be involved in either the disruption of



the partition mechanism causing excess starch accumulation or in preventing the normal degradation of starch to soluble products.

Kulshreshtha and Gopal (1983) observed that *Ceratophyllum demersum* and *Ceratophyllum muricatum* did not grow together with *Hydrilla verticillata* and that the aqueous extracts of *Hydrilla* produce allelopathic substances strongly inhibiting the growth of both *Ceratophyllum* species. *Hygrorhiza* species was also detrimental to the growth of *Ceratophyllum*.

According to Agami and Waisel (1985) bilateral negative relationships exist between *Najas* and *Myriophyllum* which seem to be of an allelopathic nature. *Najas* plants were unaffected by the presence of *Potamogeton lucens* and *Scirpus litoralis* but were significantly suppressed by *Myriophyllum*.

The aqueous extracts of *Azolla* and *Potamogeton illinoensis* however stimulated the growth of *Lemna paucicostata* at lower concentrations but reduced the growth at higher concentrations (Sutton & Portier, 1989). This indicates that at high density such plants in aquatic systems may exert chemical regulation on the growth of other plants.

According to Philips et al. (1978), *Ceratophyllum demersum* also contain allelopathic compounds that negatively influence other macrophytes.

Several studies implicate *Typha* species in allelopathic interactions (McNaughton, 1968; Szczepanska, 1971). *Typha* is found in marsh soils which could be a site of allelopathic interactions as soil toxicity is often associated with heavy poorly aerated and waterlogged soils. McNaughton (1968) reported that germination of *Typha* seeds was an almost total failure in the aqueous extract of dried *Typha* leaves. He concluded that *Typha* marshes are unlikely sites for the establishment of *Typha* seedlings as a result of the inhibitory properties of marsh soil water and that the autotoxins may be important for population regulation in these communities. He further observed that the accumulated residues in marshes could enhance the ability of toxin tolerant species to penetrate the community during the periodic droughts which become more frequent as the distance from the water table increases and reduces the ability of toxin intolerant *Typha* seedlings to become established during wetter portions of the climatic cycle. Van der Valk and Davis (1976, 1978) also found no *Typha glauca* or *Scirpus validus* seedlings in the *Typha* zones of prairie glacial marshes and suggested that allelopathic interaction accounted for this absence. Later, in a study with Indian species, *Typha angustata* and *T. elephantina*, Sharma and Gopal (1978) could not find any autotoxic effects on seed germination. In fact, seedlings were found growing within the *Typha* stands and on accumulated decomposing litter. They demonstrated that the failure of seedlings to establish in *Typha* stands is related to high light intensity requirement of the seedlings (Sharma & Gopal, 1979a,b). At the same time, Bonasera et al. (1979) reported that in a bioassay test, the root, rhizome and leaf extracts of *Typha latifolia* were least inhibitory to the growth of lettuce, radish, cucumber and tomato as compared to the extracts of three other marsh plants namely *Ambrosia trifida* (leaf), *Peltandra virginica* (leaf and petiole), and *Bidens laevis* (leaf and stem). This led to a reinvestigation of McNaughton's (1968) results by Grace (1983) who could not confirm autotoxicity in *T. latifolia* and *T. angustifolia*.

In a recent study, autotoxic effects have however been observed in *Phragmites karka* in India (Sharma et al., 1990). The germination of *P. karka* seeds was inhibited markedly in aqueous extracts of its living parts and the leachates of plant litter as well as by the soil extracts from within the *Phragmites* stand.

In *Peltandra virginica*, Whigham et al. (1979) considered allelopathy to be a factor responsible for the absence of its seedlings and plants from stream bank marshes through controlling seed germination.

Rice is the most important wetland plant cultivated around the world. There are numerous aquatic and marsh species of macrophytes which grow with the crop as weeds. There are many reports from different countries on the extent of reduction in growth by these weeds and some effort has been devoted to the understanding of this crop weed association. Whereas most of the studies emphasize on the competition for nutrients, there is growing evidence of allelochemic interactions between rice and associated macrophytes. In an interesting study, Sircar and Kundu (1959, 1960) observed that water hyacinth promotes the seed germination and seedling growth of rice and this was demonstrated to be due to the gibberellin like growth promoting substances released by water hyacinth roots (Bhanja et al., 1968; Sircar et al., 1973). Later, the aqueous extracts of various parts of *Eichhornia crassipes* were found to enhance the germination and growth of several other plants like *Cyperus rotundus* (Srivastava & Das, 1974), *Solanum melongena* (Iswaran & Sen, 1973), *Lycopersicum esculentum* (Tripathi & Srivastava, 1970), *Corchorus capsularis* (Sircar & Chakraverty, 1961), *Cicer arietinum* (Sircar & Chakraverty, 1962; Kulshreshtha, 1981) and *Spirodela polyrhiza* (Kulshreshtha, 1981).

Chou et al. (1984) clearly demonstrated that *Oryza perennis* and *Leersia hexandra* contained and exuded phytotoxic metabolites. Both the species grow in marshy habitats in the humid tropics and subtropics which are necessarily crowded by various plants if not disturbed. Such habitats would impose a pressure of density dependent mortality on the plants resulting in selection. Probably in such a condition, allelopathy helps the plants to survive the struggle for existence to some extent. Of the two species, *Leersia hexandra* was found to have a higher allelopathic potential than *Oryza perennis*.

Lee and Guh (1982) found rice plants were most damaged by *Sagittaria pygmaea* 31 to 37 days after transplanting. In a recent study, *Cyperus rotundus* and *Echinochloa colona* have been shown to inhibit the seed germination and growth of seedlings of rice (Porwal & Mundra, 1992).

Wolek (1974, 1979) investigated the influence of interaction among four species of lemnaceae. He observed that culture medium in which *Wolffia arrhiza* was kept, inhibited the growth of *Spirodela* and induced production of turions in that plant. The allelopathic influence of metabolites released by plants into the nutrient solution was stimulatory if the metabolite concentration was low. Higher concentration of metabolites caused either an indifferent or inhibiting reaction.

Elakovich and Wooten (1989a,b) screened sixteen hydrophytes, namely *Nymphaea odorata* (leaves and petioles), *Ceratophyllum demersum*, *Hydrilla verticillata*, *Eleocharis acicularis*, *Eleocharis obtusa*, *Myriophyllum aquaticum*, *Myriophyllum spicatum*, *Najas guadalupensis*, *Nymphaea cordata*, *Potamogeton foliosus*, *Sparganium americanum*, *Vallisneria spiralis*, *Brasenia schreberi*, *Cabomba caroliniana*, *Juncus repens* and *Limnobium spongia*, for allelopathic activity using *Lemna minor* as a test species. Of all the species aqueous extracts of the leaves and petiole of *Nymphaea odorata* were most inhibitory followed by *Myriophyllum aquaticum*, *Nymphaea odorata* rhizomes, and roots of *Cabomba caroliniana* and *Brasenia schreberi*. All the five species inhibited 68% or more of *Lemna minor* frond production at the lowest concentration. Chlorophyll reduction was also similarly observed by aqueous extracts of the five species. The bioassays were also performed using *Lactuca*



*sativa* (lettuce) as the test species. *Nymphaea odorata* leaves and petioles were most inhibitory followed by *Ceratophyllum* to lettuce. However, *Lemna minor* was considered to be more appropriate for use with hydrophytes. In a recent study, they found that *Nuphar lutea* ssp. *macrophyllum* was far more inhibitory than the plants examined earlier, to both lettuce seedlings and *Lemna minor* (Elakovich & Wooten, 1991). In *Lemna minor*, the growth (number) and chlorophyll content of fronds was drastically reduced by the extracts of both the leaves and below ground organs (roots & rhizomes).

#### INFLUENCE OF DEAD AND DECOMPOSING MACROPHYTES

Numerous studies of allelopathy in terrestrial environments have shown that the plant litter, intact or processed (in different stages of decomposition), and especially its leachates and extracts exert allelochemic influence on various plants of other species (Rice, 1974; Silverstein & Simeone, 1983). This has been shown to be true also in aquatic environments, particularly in littoral zones. Plant parts which do not readily decompose, accumulate on shores forming frequently thick heaps (Pieczynska, 1972). Chemical processes in such places sometimes result in pushing out the plants growing there. One of the causes may be the intoxication of the environment by allelopathic substances released after death of plants or during their decomposition. It is also important whether the decomposition of plant remains occurs in aerobic or anaerobic conditions. Patrick et al. (1964) suggest that under aerobic conditions the organic compounds disappear rapidly and microbial material is synthesized. When oxygen is deficient, volatile fatty acids and other organic acids accumulate and synthesis of microbial material is suppressed.

Szczepanska (1971) observed that the remains of several macrophyte species inhibit the growth of seedlings of *Phragmites australis* (= *P. communis*). Later, in an experimental study, she cultivated *Phragmites communis* (= *P. australis*) and *Typha latifolia* on mud with added remains of *Glyceria maxima*, *Phragmites* and *Typha*. Large amounts of plant litter was found to inhibit the growth of test species initially for 20 days after which the growth was normal (Szczepanska, 1977a). This indicates that the inhibitory substances decomposed within 20 days. Further studies showed that *Carex elata* and *Glyceria maxima* stimulate the growth of *Phragmites* whereas other species like *Eleocharis palustris*, *Schoenoplectus lacustris*, *Typha latifolia* and *Equisetum fluviatile* had an inhibiting effect (Szczepanska, 1977b).

Carter and Grace (1986) investigated the effects of aqueous leachates of shoots of *Justicia americana* on the germination, seedling growth and established plant growth of *Polygonum lapathifolium*. Both the species are common in seasonally variable aquatic habitats. When the water levels decline, the litter of *Justicia* decomposes on the exposed mudflats where most emergent aquatic species typically germinate and establish. The leachates of *Justicia* litter in concentrations comparable to those estimated for natural stands, did not affect seed germination and transplant growth but inhibited the seedling growth. When the leachates were diluted, the seedling growth was enhanced and germination remained unaffected. It was emphasized that the seedling stage of plant life cycle is most susceptible to permanent effects by chemicals released from decomposing litter and therefore, *Justicia* could restrict the growth of *Polygonum*.

The production of allelopathic substances during decomposition of rice straw has

been investigated in some detail. Chou et al. (1987) have shown that the litter of rushes also undergoes various chemical changes during decomposition and may have inhibitory effects.

An interesting allelopathic substance which inhibits growth of *Hydrilla verticillata* has been found in the peaty sediments of swamps dominated by *Taxodium distichum* (Bartrop & Martin, 1983; Dooris & Martin, 1981; Dooris et al., 1988). The substance, suspected to be a polyphenolic compound (Dooris & Martin, 1985; Martin, 1983) has also been observed to inhibit the growth of *Scenedesmus obliquus* (Dooris et al., 1982). There has been no attempt to find the source of this substance which may be derived from any of several aquatic plants.

#### AQUATIC-TERRESTRIAL PLANT INTERACTIONS

##### *Effects of Macrophytes on Terrestrial Plants*

Several aquatic macrophytes have been observed to inhibit the germination and/or seedling growth of various terrestrial crop plants. *Lactuca sativa* is indeed used as a bioassay for testing allelopathy among aquatics due to its being most sensitive to such substances. However, there are no reports of allelopathic effects of aquatic plants upon the vegetative and reproductive growth or the yield of any terrestrial plant so far. The available information provides strong evidence that aquatic angiosperm leachates contain substances that prevent, inhibit or have a negative impact upon germination and seedling development of some terrestrial plants which differ in their sensitivity to the aquatic plant leachates.

Singh (1968) reported the presence of a growth inhibitor in the tubers of *Cyperus rotundus* which is a widespread weed of both terrestrial and aquatic habitats. Kulshreshtha (1981) observed that the aqueous extracts of roots, rhizome and leaves of *Phragmites karka* inhibit the growth of seedlings of wheat, barley, pea, and chickpea. However, the extracts of *Vallisneria* and *Potamogeton pectinatus* as well as water hyacinth promoted the growth of wheat seedlings. Singhvi and Sharma (1984) reported that the extract of different plant parts of *Ipomoea aquatica* inhibit the growth and biomass of *Pennisetum typhoideum* whereas *Ludwigia adscendens* seems to stimulate growth. They suggested that the growth promoting effect may be due to terpenoids and the growth inhibiting effect may be due to phenols.

El-Ghazal and Reimer (1986) examined the effects of *Cabomba caroliniana*, *Elodea nuttalli*, *Myriophyllum* sp., *Spirodela polyrhiza* and *Vallisneria americana* on four terrestrial species (*Lactuca sativa*, *Triticum aestivum*, *Echinochloa crusgalli*, *Ipomoea hederacea*). *Lactuca* was found to be most sensitive. The extract of *Vallisneria* markedly inhibited seed germination, seedling growth and chlorophyll production in lettuce (*Lactuca sativa*) (Cheng & Reimer, 1988, 1989).

Kleiven and Szczepanska (1988) studied the effect of extracts of *Chara tomentosa*, *Ceratophyllum demersum* and *Myriophyllum verticillatum* on seed germination and seedling growth of *Lepidium sativum*. Extracts of *Chara* strongly inhibited shoot growth and leaf development of *L. sativum*. The active substances were temperature stable and low molecular weight compounds. *Ceratophyllum* extracts were less inhibitory and those of *Myriophyllum* were not inhibitory to *Lepidium* seeds.

In another study, Drost and Doll (1980) observed that the residues of *Cyperus esculentus* tubers and foliage reduced the growth (dry weight) of corn and soybeans.

At equal concentrations tubers were more effective than the foliar residues, and soybean was more adversely affected than corn.

### *Effect of Terrestrial Plants on Macrophytes*

Little is known of the allelopathic effects of terrestrial plants on the aquatic species. Holm (1969) described examples of allelopathic interactions in a Dutch polder where *Catabrosa aquatica* and *Tussilago farfara* repressed the growth of surrounding species of *Phragmites* and *Senecio*. In recent years, the allelopathic potential of a terrestrial weed, *Lantana camara*, has been reported against a number of aquatic plants. *Lantana* is well known for its allelopathic nature against many terrestrial plants (Achhireddy & Singh, 1984) and the chemical nature of its allelochemicals has also been studied in considerable detail. Sutton and Portier (1989) reported that the green and brown (dead) *Casuarina* needles and leaves of *Lantana camara* and *Stenotaphrum secundatum* inhibit the growth of *Lemna paucicostata*. Jain et al. (1989) confirmed the inhibitory effect of *Lantana* leaves on *Lemna minor*, and isolated several phytotoxins of which 14 phenolic compounds were identified in the extracts. These were protocatechic acid, gentisic acid, vanillic acid, caffeic acid, syringic acid, vanillin, m-coumaric acid, p-coumaric acid, o-coumaric acid, ferulic acid, t-cinnamic acid, methyl coumarin and salicylic acid. The acidic extract contained p-hydroxybenzoic acid as the most abundant but the least inhibitory phenolic compound, p-coumaric acid was most abundant in the neutral and basic extracts but salicylic acid was the most toxic substance.

Recently Saxena (1991, 1992) observed that the extracts of *Lantana*, both live and air dried, inhibit the growth of *Spirodela polyrrhiza*, *Salvinia molesta* and *Azolla pinnata*. The extract is highly toxic to water hyacinth which is completely killed within a few days.

Among other terrestrial plants, leaf leachates of *Eucalyptus* species which have received considerable attention for their allelopathic properties (Kohli et al. 1987; May & Ash, 1990; Singh & Kohli, 1992), have also been found to inhibit the growth of a number of aquatic plants including duckweeds.

In some cases, terrestrial leaf litter has been found to stimulate the growth of aquatic plants. Sinhababu and Kushari (1984) reported that the leaf leachates of *Polyalthia longifolia* promoted the growth and nitrogen fixation in *Azolla pinnata*. Kushari (1987) observed that the leaf leachate of *Azadirachta indica* not only promoted the growth of *Azolla pinnata* but also protected it from attack by insects and snails. Similarly, the leaf leachates of both *Azadirachta indica* and *Albizia lebbek* have been found to stimulate the growth of *Eichhornia crassipes* as well (Taheruzzaman & Kushari, 1991).

### MACROPHYTE-MICROPHYTE INTERACTIONS

#### *Macrophytes and Phytoplankton*

The interactions between macrophytes, particularly the submerged species, and the microphytes (phytoplankton and epiphytes) have been a subject of considerable interest and debate among limnologists. Both macrophytes and phytoplankton are suppressed by the other under certain conditions.

It is a common observation that a dense growth of submerged macrophytes suppresses phytoplankton (as well as filamentous algae) and death of macrophytes (such as that after herbicide application) results in rapid bloom formation. The suppression of phytoplankton by *Elodea canadensis* was described first by Schreiter (1928). Later, Hasler and Jones (1949) reported that *Potamogeton foliosus* and *Elodea canadensis* were antagonistic to the growth of planktonic blue green algae. Guseva and Gonchrova (1965) observed that the presence of macrophytes favours the growth of some blue green algae whereas Kogan and Chinnova (1972) found inhibition of other algal groups by *Ceratophyllum demersum*. According to Fitzgerald (1969), aquatic macrophytes had a growth inhibiting effect on microalgae when the nutrients were limiting. Suppression of phytoplankton blooms by *Chara* species has been recorded by Crawford (1979) in prairie ponds and more recently by Horecka (1991) in a Pannonian lake (Czechoslovakia). These phenomena have been explained on the basis of allelochemic influences or competition for light and nutrients or both. Goulder (1969) ascribed competition for nutrients as the major factor in the succession from phytoplankton to a thick mat of *Ceratophyllum demersum* which could later inhibit phytoplankton growth by shading. Steemann-Nielsen (1973) who observed an extraordinary low primary productivity of the phytoplankton in a brackish water area with extensive *Chara* populations, considered allelopathy to be an important factor. Philips et al. (1978) explained that dense macrophyte beds were due to suppression of phytoplankton by allelopathic substances from macrophytes or by competitive nutrient uptake by macrophytes. They could not confirm the existence of organic suppressors but hypothesized that when excess nutrients are available, the phytoplankton get sufficient nutrients to overcome the inhibition from the macrophytes. Brammer (1979) who observed suppression of phytoplankton by submerged *Stratiotes aloides*, concluded that competition for nutrients, rather than allelopathy, seemed to be a more likely explanation for the decline in phytoplankton. Wetzel (1983b) remarked that "macrophytes may influence the competition of blue green algae with other algal groups by blue-green heterotrophic utilization of certain excreted organic compounds." Elakovich and Wooten (1987) found evidence in favour of allelopathy in a floating leaved macrophyte, *Brasenia schreberi* which inhibits lateral growth of the eukaryotic alga *Chlorella pyrenoidosa* and the prokaryotic alga *Anabaena flosaque*. It was suggested that *Brasenia* gains dominance in aquatic environments due to its phytotoxic properties.

Similarly, there are several studies on the suppression of macrophyte growth by different algae, especially thick algal blooms of bluegreen algae which develop in eutrophic waterbodies. Jupp and Spence (1977) observed the decline of macrophytes in Loch Leven and attributed it mainly to the high phytoplankton densities which develop during the summer months due to high input of phosphorus in the area. It was observed that competition from algal blooms between May and October adversely affected the biomass of *Potamogeton filiformis* and the inhibitory effect could be partly due to the poor underwater light by high chlorophyll levels. When the bloom consists of buoyant blue green algae such as *Anabaena* sp. which can form dense floating scum over macrophyte beds, the underwater light is further reduced and these retard the macrophyte growth.

The studies of Moss and his coworkers (see Moss 1989) show that the interactions between phytoplankton and macrophytes are rather complex as the herbivore zooplankton and fish can also influence them. Extensive field and experimental investi-

gations on the macrophyte decline and phytoplankton blooms in eutrophic waters demonstrate that even under eutrophic conditions phytoplankton populations may not appear because they are actively grazed upon by zooplankton. On the other hand, the presence of planktivorous fish may result in phytoplankton blooms due to depletion of the herbivore populations.

However, several studies do suggest the possibility of allelopathic influences of planktonic algae on macrophytes (Jones et al., 1983). Kirpenko (1986) reported the blue-green alga, *Microcystis aeruginosa*, to be toxic in fairly low concentrations to *Elodea* and duckweeds. Sharma (1985) recently reported that the growth of *Eichhornia crassipes* was inhibited when grown in water containing planktonic algae such as *Scenedesmus bijugatus*, *Chlorella pyrenoidosa* and species of *Aphanothece*, *Euglena*, *Merismopedia* and *Coelastrum*. The size of plants, their dry weight, chlorophyll *a* and *b* contents and their rate of vegetative propagation were very much reduced compared with control plants grown in algae free water. The hyacinth plants ultimately died after 90–100 days of growth with algae. The adverse effect on growth of waterhyacinth was considered to be due to allelochemicals produced by the algae though no explanation was offered for the probable mechanism.

The production of allelochemical substances by phytoplankton and their role in algal succession have been demonstrated in many studies (Gross et al., 1991; Jüttner, 1981; Keating, 1977; Maestrini & Bonin, 1981; Wetzel, 1983b). It is quite likely that these compounds are also active against some macrophytes, and hence, the role of allelopathy cannot be ruled out.

Filamentous algae have also been observed to influence the growth of macrophytes adversely. Goulder (1969) found that growth of shoot apices of *Ceratophyllum* was retarded and some of them broke down when *Spirogyra* was entangled around them. In another study, restriction of growth of *Najas marina* by *Spirogyra* has been demonstrated in laboratory experiments, and the disappearance of *Najas* was correlated with the development of extensive mats of *Spirogyra* (Phillips et al., 1978).

The ability of a plant to photosynthesize effectively in changing conditions may influence its competitive success. Allen and Spence (1981) and Maberly (1983) suggested that the algae may generate high pH values in bright conditions to adversely affect the aquatic plants with lower affinity for bicarbonates and water quality may be affected which gives *Cladophora glomerata* a competitive advantage over *E. canadensis*. Simpson and Eaton (1986) suggest another way in which filamentous algae can be put at an advantage over a vascular competitor. Algae like *Spirogyra* and *Cladophora glomerata* induced high oxygen, high pH and low carbon dioxide conditions in the water and put vascular macrophytes like *Elodea canadensis* under photosynthetic stress while the algae are less affected. Algae depress the photosynthetic activity of *E. canadensis* leading to the latter being outcompeted.

*Cladophora* has been found to cause increased mortality and a decline in area of *Phragmites australis* in several European waterbodies. Extensive experiments on the effect of decaying *Cladophora* on the sprouting of rhizomes and growth of roots and shoots have shown that the alga is allelopathic to the reed (Schroeder, 1987). More recently, Ozimek et al. (1991) observed that the growth of *Elodea canadensis* was reduced by 35 to 57% in the presence of *Cladophora glomerata*. The alga decreased the growth of new shoots and accelerated the decay of old shoots. However, the alga did not affect the growth of *Potamogeton pectinatus*.



*Macrophytes and Epiphytes*

Macrophytes are often colonized by a rich array of algae, microbes and consumers particularly in hard water lakes where carbonate deposits provide a matrix for the epiphytes (Allanson, 1973). The mutual relationships of the macrophytes and their epiphytes have remained controversial. Several studies have generated evidence in favour of a neutral substrate hypothesis according to which the macrophytes exert no more influence on the epiphytes than providing a substrate for attachment (Blindlow, 1987) whereas others have shown that the physicochemical changes in the water mediated by the macrophytes govern the epiphytes (O'Neil Morin & Kimball, 1983). Yet, there is enough evidence from both field and experimental studies that the diversity and function of epiphytes are influenced by the type of macrophytes (Eminson & Moss, 1980) and that the epiphytes contribute significantly to the nutrient dynamics of the aquatic systems.

It has been demonstrated that the organic carbon released by macrophytes is a major substrate for epiphytes (Allen, 1971; Sondergard, 1983). However, the living macrophytes release very little phosphorus (Barko and Smart, 1980; Smith, 1978) and epiphytic algae obtain less than 10% of their phosphorus from the host macrophyte (Carignan & Kalff, 1982). On the other hand, epiphytic algae rapidly assimilate phosphorus released from decomposing macrophytes (Burkholder & Wetzel, 1990; Howard-Williams & Allanson, 1981). Thus, organic carbon and phosphorus behave somewhat differently in the macrophyte-epiphyte complex. According to Howard-Williams (1981), the epiphytes appear to be much more active than their hosts in dissolved nutrient exchanges with the water.

Many invertebrates associated with the macrophytes eat the epiphyte-detritus complex on the surface of macrophytes rather than the macrophyte itself (Cattaneo, 1983; Orth & Van Montfrans, 1984; Reavell, 1980). It has been suggested that the epiphytes benefit macrophytes because they distract grazers from the latter (Hutchinson, 1975). Epiphytes do not defend macrophytes from grazers; instead epiphytes are preferred over macrophytes because many aquatic grazers do not have mouth parts capable of puncturing or tearing macrophyte tissues or these may be unpalatable to grazers. Macrophytes in turn benefit epiphytes by providing a substrate and nutrients. Thus selection has favoured macrophytes that leak organic carbon and other nutrients and stimulate epiphytic growth (Wetzel, 1983a).

Excessive epiphytic growth, however, decreases macrophyte photosynthesis (Bulthuis & Woelkerling, 1983; Phillips et al., 1978) by intercepting light and influencing exchange of nutrients and gases. Some macrophytes have apparently developed strategies to avoid such interference with growth by the epiphytes. *Zostera marina*, a fast growing macrophyte, is able to produce up to 6 cm of new leaf each day. The new leaf surface is covered by a single epiphyte layer 5–10 days after its appearance. So most of the surface of the plant remains unshaded and it is able to carry out maximum photosynthesis under unfavourable conditions (Wium-Anderson & Borum, 1980, 1984). In *Juncus bulbosus*, the life cycle itself reflects a strategy to avoid competition for inorganic carbon with epiphytes and other primary producers in the lake (Svedang, 1990).

Allelopathy offers another useful alternative to avoid competition. *Chara* is often found in monotypic stands and gives an insight into the very delicate balance between the submerged vegetation, epiphytes and phytoplankton discussed by Philips et al.

(1978). Stands of *Chara globularis* in Swartvlei (S. Africa) are generally devoid of or with very few epiphytes (Howard-Williams, 1978). In Danish lakes, the stands of *Chara*, *Nitella*, *Tolypella* and *Ceratophyllum*, *Batrachium*, *Stratiotes* and *Berula* are often almost free of epiphytes (Wium-Anderson, 1987; Wium-Anderson et al., 1982). Allelopathy has been demonstrated to be the major factor and the allelopathic compounds released by the charophytes have been also isolated (Wium-Anderson, 1987). However, in a recent study, Forsberg et al. (1990) could not confirm the allelopathic effects of *Chara* on phytoplankton in natural conditions. They found sufficient quantities of epiphytes including diatoms and cyanophytes on *Chara* sp. which were similar to those on *Potamogeton* sp. The phytoplankton populations were shown to be related to the phosphorus levels in lake water.

#### IV. Macrophyte-Macroinvertebrate Interactions

A large variety of invertebrates is commonly associated with macrophyte communities. Most of the macrophytes support the growth of epiphytic algae and bacteria which are major constituents of food of the invertebrates. Various invertebrates, including larval stages of insects (Diptera, Coleoptera, Hemiptera, Ephemeroptera), also consume the macrophytes living or in different stages of decay (Gaveskaya, 1969; Sankaran & Rao, 1972). The dissolved organic matter released by the plants is also an important source of nutrients (Wetzel, 1983a). Further, the macrophytes provide shelter to the animals from inimical forces, and substrate for oviposition and often for gaining access to air-water interface. Submerged macrophytes provide oxygen during day time and remove toxic factors such as ammonia and carbon dioxide. Thus, the densities of both the zooplankton and other invertebrates is generally higher among the macrophyte communities than in the open water (Pennak, 1966). However, invertebrates do not simply benefit from the macrophytes. Their interactions are often complex and interesting.

As early as 1921, *Myriophyllum* sp. was shown to have repellent properties against *Anopheles mosquitoes* (Bachmann, 1921). Hasler and Jones (1949) observed that some submerged macrophytes were antagonistic to rotifers but not to planktonic crustacea. Pennak (1973) however reported that *Daphnia rosea* was strongly repelled by *Elodea*, *Nitella* and *Myriophyllum*. Since then many studies have demonstrated that some submerged macrophytes release chemical substances which repel or strongly inhibit the growth and development of various zooplankton (Dorgelo & Koning, 1980). The insecticidal effects of Charophytes (species of *Nitella*, *Chara*, *Tolypella*), particularly against mosquitoes, have been widely reported (Jacobsen & Pedersen, 1983; for review see also Hutchinson, 1975). Other macro-algae like *Cladophora* also have adverse effects on the mosquito larvae (LaLonde et al., 1979). In a detailed study, Dhillon et al. (1982) observed that *Myriophyllum spicatum* growing profusely in stagnant water habitats regulates population density of chironomid midges. The plant extract was found to be toxic to the first and fourth instar larvae of several mosquitoes (*Culex quinquefasciatus*, *Culex tarsalis*, *Culiseta incidens* and *Aedes aegypti*) and chironomid midges. High mortality in all the species occurred at a low concentration, and at a higher concentration, 100 percent mortality was recorded. Among chironomids, *Tanytarsus* sp. was more tolerant to the extract than *Chironomus* sp. The plant extract however had an unique property as it acted as an attractant to the adults of *Culex quinquefasciatus* and *Aedes aegypti*.



The interactions of macrophytes (as well as their epiphyte association) with molluscs have received considerable attention. Molluscs are not only among the most abundant invertebrate fauna in macrophyte stands (Akhtar, 1978; Junk, 1977; Krishnamoorthi et al., 1968, O'Hara, 1967), they assume greater significance because several molluscs are vectors of dreaded human diseases like Schistosomiasis and Bilharziasis. The positive association between molluscs and macrophytes is confirmed by the drastic reduction in mollusc populations after removal of macrophytes (Pimentel & White, 1959; Van Schayck, 1985).

Whereas some gastropod molluscs feed directly on macrophytes and may cause major reduction in their biomass, and even their disappearance (Sheldon, 1987), others feed on the decaying plants or the epiphyton of plant surface. Several studies show that the molluscs help macrophytes by removing excessive epiphyte growth and senescing macrophyte tissue, thereby reducing shading (Hootsmans & Vermaat, 1985; Howard, 1982; Howard & Short, 1986; van Montfrans et al., 1982, 1984) and removing the pathogenic fungi and bacteria which may invade healthy tissues (Rogers & Breen, 1983; Underwood, 1989). The conditioning of plant surface by snail mucus may also reduce the probability of attack by insects or other herbivores. Brönmark (1985, 1989) reported that the growth rate of *Ceratophyllum demersum* increased in the presence of epiphyton feeding snail, *Lymnaea peregra*. The enhancement of macrophyte growth has been demonstrated even when the snails were not in direct contact with the plants (Underwood, 1989). These mutualistic interactions often exhibit specificity inasmuch as various molluscs are associated with specific macrophytes. For example, Dazo et al. (1966) found that *Biomphalaria alexandrina* and *Bulinus truncatus* were closely associated with *Potamogeton crispus* and *Eichhornia crassipes*. Significant positive association was noted between *Alternanthera sessilis* and *Bulinus forskali* and *Bulinus rophlfsi*, *Lemna paucicostata* and *Bulinus forskali* (Ndifon, 1979; Ndifon & Ukoli, 1989), and *Lymnaea truncatula* and *Glyceria fluitans*, *Juncus inflexus* and *Ranunculus repens* (Moens, 1981). *Planorbis vortex* is associated with long lived species like *Glyceria maxima* whereas *Lymnaea peregra* lives among relatively short-lived submerged *Elodea canadensis* (Lodge, 1985, 1986). In Nigeria, *Biomphalaria pfeifferi*, *Bulinus forskali* and *Anisus coretus* have positive association with *Nymphaea lotus* (Thomas & Tait, 1984) and *Biomphalaria glabrata* is commonly associated with *Ceratophyllum demersum* in Africa and S. America (Thomas, 1987).

Detailed experimental and biochemical studies have demonstrated that the macrophyte-mollusc interactions are regulated by allelochemicals which act as repellents, attractants or arrestants. Sterry et al. (1983), in their study of *Biomphalaria glabrata*, observed that *Ceratophyllum demersum*, *Hippuris vulgaris* and *Nasturtium officinale* were strongly repellent, *Lemna trisulca* and *Elodea canadensis* were neutral and *Lemna paucicostata* produced a strong attractant to the mollusc. It was observed that decaying *Lemna paucicostata* was a significantly stronger attractant and arrestant, and that this effect was due to short chain (C<sub>2</sub>-C<sub>5</sub>) carboxylic acids which were produced during decomposition (Patience et al., 1983). The concentration of these acids increased during the course of decomposition. Some carboxylic acids are also produced by decomposing *Ceratophyllum demersum* and act as attractants for *Biomphalaria* (Sterry et al., 1985). Brönmark (1985) also confirmed that *Ceratophyllum demersum* excretes dissolved organic matter which acts as an attractant for *Lymnaea peregra* though the plant itself is protected against herbivory by a

repellent. For a recent detailed account of the interactions in a macrophyte-epiphyte-mollusc association, see review by Thomas (1990).

## V. Allelopathy of Macrophytes Against Bacteria

The allelopathic activity of the macrophytes is further demonstrated by the antimicrobial properties of the exudates of many species. Drobot'ko et al. (1958) and Belt'yukova and Pastushenko (1963) reported antimicrobial activity of the alkaloids from *Nuphar luteum*. Detailed field and laboratory studies of Seidel in Germany demonstrated the antimicrobial activity of the root exudates of a number of aquatic macrophytes like *Scirpus lacustris*, *Acorus calamus*, *Juncus effusus*, *Juncus maritimus*, *Iris pseudoacorus*, *Mentha aquatica*, *Phragmites communis* and also the root nodules of *Alnus glutinosa* (Seidel, 1965, 1969, 1971a, 1972, 1973, 1974). Stangenberg (1968) reported bacteriostatic activity in some extracts of *Lemna minor* against *Sphaerotilus natans*. Su et al. (1973a,b) and Su and Staba (1973) investigated the antimicrobial activity of extracts of 24 macrophytes against several bacteria and fungi. The ethanol or chloroform extracts of *Nymphaea tuberosa* had high antimicrobial activity against *Mycobacterium smegmatis*, *Staphylococcus aureus*, *Alternaria* sp. and *Fusarium roseum*. The antimicrobial compounds were identified as tannic acid, gallic acid and ethyl gallate. Among other macrophytes with very high antimicrobial activity were *Carex lacustris* (against *Staphylococcus aureus*, *Mycobacterium smegmatis* and *Alternaria* sp.), *Vallisneria americana* against *Candida albicans*, *Lemna minor*, *Potamogeton natans*, *Potamogeton zosteriformis* and *Typha angustifolia* against *Alternaria* sp. More recently, Elakovich and Wooten (1987) reported the antibacterial properties of *Brasenia schreiberi* against a number of bacteria including *Chromobacterium violaceus*, *Staphylococcus aureus*, *Escherichia coli*, *Mycobacterium smegmatis* and *Salmonella gallinarum*. Potentially antimicrobial compounds have been isolated from several other aquatic angiosperms (Harrison & Durance, 1985; McMillan et al., 1980).

## VI. Chemical Nature of Alleochemicals

Reviews by Harborne (1977), Putnam (1983) and Rice (1979, 1984) of the chemistry of various allelochemical compounds in terrestrial ecosystems, show that a wide range of chemical compounds have been implicated in allelopathy, e.g. alkaloids, flavanoids, phenolic acids, aliphatic acids, glycosides, terpenoids, lactones, tannins, organic acids and sugars. Most of them are secondary metabolites and are released into the environment either by leaching, volatilization or exudation from shoots and roots. Many compounds are degradation products and are released during decomposition of dead tissues. The secretion and leaching of organic compounds from living aquatic plants, both macro- and microphytes, has been frequently observed (Wetzel, 1969; Wetzel & Hough, 1973). McClure (1970) reviewed in detail the distribution and chemistry of secondary metabolites in aquatic plants. It is interesting that alkaloids are the dominant secondary metabolites in rooted floating leaved species (most of the Nymphaeaceae) whereas flavonoids dominate among free floating species. Terpenoids are usually common in species that occur on waterlogged soils or relatively drier margins of the waterbody (like Cyperaceae, Graminae and Acanthaceae). The submerged and emergent taxa contain both simple phenols and flavonoids. However, there are only few

studies on the nature of substances in plants whose allelopathic activity has been specifically demonstrated. It is largely due to the fact that the isolation and identification of allelochemicals is a laborious time consuming exercise. For isolation of compounds, plants are extracted with different organic solvents and the dissolved substances are separated. The active fractions are singled out through bioassay experiments. The separation is continued until a pure sample is obtained. Then, the purified substances are identified by various analytical techniques using Gas Chromatography, Mass Spectrometry and Nuclear Magnetic Resonance (NMR) (Anthoni et al., 1980; Wium-Anderson, 1987). And, finally, the allelopathic activity of the isolated substances is confirmed experimentally at concentrations expected to occur in nature. All these steps have rarely been taken in the case of aquatic plants.

#### LONG-CHAIN FATTY ACIDS

Long chain fatty acids appear to be characteristic of aquatic plants. The first allelochemicals produced by the alga, *Chlorella* were found to be fatty acids (Spoehr et al., 1949). Proctor (1957) suggested that the inhibitor of other algae produced by *Chlamydomonas reinhardi* is a long-chain fatty acid or a mixture of such acids. McCracken et al. (1980) identified fifteen 14–20 carbon fatty acids. Alsaadwi et al. (1983) reported for the first time the involvement of long chain fatty acids in allelopathic interactions in *Polygonum aviculare*. Van Aller et al. (1983) found fatty acids to occur in members of Cyperaceae. They isolated C–20 trihydroxycyclopentyl and C–18 hydroxycyclopentenone fatty acids from *Eleocharis microcarpa* (Van Aller et al., 1985) and identified them using various chemical and spectral methods. The compound was characterized as 11-hydroxy–14 (3,5-dihydroxy–2 methylcyclopentyl)-tetradec–9-ene–12-yneic acid. These components were also extracted from pond waters where plants were actively growing indicating that the chemical substances are actually released by the aquatic macrophytes into water. The oxygenated fatty acids (OFA) from *E. microcarpa* were in higher concentration during the early summer when maximum growth occurred. Bioassays of the OFA mixture against various algae showed them to have good specificity against blue green algae. These compounds may therefore be also significant in algal succession.

*Potamogeton*, *Najas*, *Thalassia* sp. and *Ruppia* species were also found to contain oxygenated fatty acids in small amounts. These plants exert definitive effects on the phytoplankton community in eutrophic systems by showing selective inhibition against blue green algae.

Stevens and Merrill (1980) isolated and identified a phytotoxic compound dihydroactinidiolide (DAD) from *Eleocharis coloradoensis*, and then synthesized it. DAD was observed to be highly inhibitory for *Nasturtium officinale* and *Raphanus sativus* in bioassays. Later, Ashton et al. (1985) observed that the most active allelopathic fraction in *Eleocharis coloradoensis* extract was peak 1B of the polar portion. The molecular weight of the compound was between 600 and 1000 but the exact compound could not be identified. Fatty acids have also been found in *Typha latifolia* (Aliotta et al., 1990).

#### ALLOMONES

Some species of charophytes have a strong, pungent smell indicating the presence of allomones. Anthoni et al. (1980) isolated 4-methylthio–1,2-dithiolane and 5-

methylthio-1,2,3-trithiane from *Chara globularis*. The substances, synthesised later by Anthoni and Christophersen (1982) were found to strongly inhibit photosynthesis of epiphytic diatom, *Nitzschia palea* and other phytoplankton at concentrations of only 2–3 M (Wium-Anderson et al., 1982). The phytotoxins had insecticidal properties when applied to *Musca domestica*, *Sitophilus granarius* and *Drosophila melanogaster* (Jacobson & Pedersen, 1983). This could account for inhibition of oviposition by mosquitoes in containers with *Chara* as mentioned by Hutchinson (1975). Photosynthesis inhibiting substance, Dithiolane has been found in *Nitella* also. Allomones are also known to occur in rice as defense against stem borers (Dale, 1992).

#### ELEMENTAL SULPHUR

Sulphur compounds are rare in higher plants but occur in cruciferae (mustard oils) (Bell & Muller, 1973; Evenari, 1949). In aquatic environments, the allelopathic relationship of elemental sulphur has been shown since it was isolated from the red alga *Erythrophyllum dilesseroides* (Izac et al., 1982) and *Ceramium rubrum* (Iakawa et al., 1973). Wium-Anderson et al. (1982) reported the release of elemental sulphur from *Ceratophyllum demersum*. It has strongly algicidal properties as it is ten times more toxic to algae than the trithiane compound released from *Chara*. Wium-Anderson et al. (1983) have proposed that sulphur released from *C. demersum* acts as an allelopathic agent which accounts for the low epiphytic growth on the macrophyte.

#### PHENOLS AND THEIR DERIVATIVES

Phenols are among the most common phytotoxic compounds found in many plants. Harborne (1977) suggested that the role of phenolic compounds in living tissue is that of preparing a chemical barrier against microbial invasion. Because of the water soluble nature of the most phenolic compounds, their release from dead tissues may be one of the ways of interference in aquatic plants. A survey of seagrasses indicates that sulphated phenolic compounds occur widely among populations of diverse marine habitats, and may play a role in the adjustment to the seawater habitat as well as in the allelochemic relations of seagrasses (Zapata & McMillan, 1979). Quackenbush et al. (1986) reported the presence of six phenolic acids (ferulic, vanillic, hydroxybenzoic, caffeic, gallic, protocatechic and gentisic acids) in aqueous extracts of *Zostera marina* using High Performance Liquid Chromatography.

The effects of phenolic compounds on growth and metabolism of aquatic macrophytes are poorly understood (Stom & Roth, 1981). Phenols in high concentrations are injurious to algae and aquatic spermatophytes. Some aquatic plants like *Scirpus lacustris* are able to eliminate phenolic compounds (Seidel, 1965, 1971b; Werner & Pawlitz, 1978) and even metabolise them (Seidel, 1971b; Seidel & Kickuth, 1970). McNaughton (1968) had suggested that phenolic compounds are the principal active agents in preventing seed germination in a marshy environment. Drost and Doll (1980) observed that plant extract of *Cyperus esculentus* contains a number of different phenolic compounds. The active phenolics are: p-hydroxybenzoic, vanillic, syringic, ferulic and p-coumaric acids (Jangaard et al., 1971; Sanchez et al., 1973). They also identified salicylic, protocatechic and caffeic acids and eugenol. An allelopathic phenolic compound has also been reported from growing *Cyperus rotundus*.

Flavonoids are widely occurring secondary metabolites among members of Lemnaceae (McClure, 1970; McClure & Alston, 1964). Wallace et al. (1969) observed that when members of Lemnaceae are grown on defined media under axenic conditions, cinnamic acids are quickly detected in the medium and after several days flavanoids are formed. Pridham (1964) reported the formation of high concentration of glycosides in emergent shoot of the rooted aquatic *Nymphaea alba*. Jurd et al. (1957) found caffeic acid esters in the medium in which free floating aquatic *Spirodela oligorhiza* was growing. Cheng and Riemer (1989) partitioned the aqueous extracts of *Vallisneria americana* into neutral, acidic and basic fractions. By using HPLC, gallic, vanillic, p-coumaric and ferulic acids were identified in the neutral fraction. Gallic and vanillic acids were the main components whereas p-coumaric acid and ferulic acids were present in lower concentrations. This plant also exhibited allelopathic properties when applied as mulch. Reznik and Neuhausel (1959) have observed the presence of caffeic and chlorogenic acid in *Elodea canadensis*. Caffeic acid was also observed in *Stratiotes* (Bate Smith, 1968). The rare 4-arylnaphthalene derivatives Justicidin A and B which are extremely poisonous for fish, were extracted from *Justicia* species (Munakata et al., 1965).

#### ALKALOIDS

Alkaloids are well known to occur widely in members of Nymphaeaceae such as species of *Nuphar*, *Nymphaea* and *Nelumbo* (Wrobel, 1967). Several sulphur containing alkaloids such as neothiobinupharidine occur in *Nuphar* species (Achmatowicz & Bellen, 1962). Ostrofsky and Zettler (1986) observed the presence of alkaloids in all fifteen species of Nymphaeaceae examined. They observed that the concentration of alkaloids was low (0.13–0.56 mg/g dry wt) but high enough to defend the plants from herbivores in waterbodies. According to Smock and Stoneburner (1980) the aquatic plants are not much grazed when alive. This may be due to the presence of defensive chemicals such as alkaloids which tend to be labile.

#### STEROIDS

Della Greca et al. (1990) extracted an antialgal sterol with an unusual 20S configuration from *Typha latifolia*. The allelochemical, identified as (20S)-4 $\alpha$ -methyl-24-methylenecholest-7-en-3- $\beta$ -ol inhibited *Anabaena flosaquae* and *Chlorella vulgaris*. More recently, Aliotta et al. (1990) isolated two more sterols,  $\beta$ -sitosterol and stigmast-4-ene-3,6-dione, from *Typha latifolia*.

#### OTHER COMPOUNDS

Besides the above compounds, several other substances have been occasionally reported. Gibbs (1974) reported the presence of a cyanogenic compound in *Myriophyllum*. Godmaire and Nalewajko (1990) detected high carbohydrate content and free sugars in *Myriophyllum* trichomes and lipophilic substances were also observed. *Elodea*, *Stratiotes* and *Berula* have also been found to release chemical substances inhibitory for photosynthesis but the active substance has not yet been identified. Terpenoids along with phenolics have also been detected in *Cyperus rotundus* (Willaman & Schubert, 1961).

## VII. Competition, Allelopathy and Community Organization

### COMPETITION

Since Clements (1904), community ecologists have laid considerable emphasis on the role of competition in regulating the structure and dynamics of the communities. It has been recognised as a predominant factor by some (Grime, 1979; Tilman, 1988) whereas its dominance over other controlling factors is questioned by others (Austin, 1990; Connor & Simberloff, 1979, 1983; Hairston et al., 1960; Simberloff, 1983). The studies on competition among aquatic plants summarised here, instead of helping to resolve the issue, appear to leave a question mark on the occurrence of competition itself. As Connell (1990) puts it, "the first task is to demonstrate unequivocally its occurrence in nature, yet this has often proved to be difficult."

Buttery and Lambert (1965) concluded that competition produced the vertical zonation of *Glyceria maxima* and *Phragmites australis* (= *P. communis*). Grace and Wetzel (1981) and Grace (1987, 1988) also demonstrated that interspecific competition determined the vertical distribution of two species of *Typha*. Competition has been demonstrated between different species of duckweeds and other free-floating macrophytes. However, Chambers and Prepas (1990), McCreary et al. (1983) and Moyle (1945) did not find evidence of competition. Wilson and Keddy (1991) also observed that the growth of established emergent plants was not influenced by neighbours and therefore, tried to generalise that "competition has little effect on aquatic macrophytes." They stated that "field experiments which have found competition in wetlands have all involved communities with soils at least partly above the water line." They concluded on the basis of their experimental data that "competition is more likely to be detected in shallow water than deep." Is this generalisation true? Do the terrestrial and aquatic plants differ in their response to neighbour effects? And do the submerged macrophytes behave differently from the free-floating or emergent macrophytes? If these are facts, how are the differences explained? Are there any morphological or physiological attributes of submerged plants that confer upon them the ability to downplay competition? Or is the aquatic environment responsible for this divergence? A cursory look at the information suggests that the importance of competition declines with increasing water regime from land through waterlogging to deep submergence. Alternatively, is it possible that the methodology used to study competition is not appropriate for shallow and deepwater habitats?

Currently the definition of competition itself is a subject of considerable debate (Grime, 1979; Thompson, 1987; Tilman, 1987, 1988). In the words of Grace and Tilman (1990), "definitions range from the narrow to the general, from operational to philosophical, and from phenomenological to mechanistic." Ecologists differ in their views on what constitutes competition. Whereas Harper (1977) preferred the term interference to include all the effects of neighbour including competition, Connell (1990) defines competition as "a reciprocal negative interaction between two organisms." Although Begon et al. (1986) include the 'reduction in survivorship, growth, and/or reproduction' among the effects of competition, most of the studies concentrate only on biomass. It is interesting to note that Wilson and Keddy (1991) observed that the presence of neighbours adversely affected the establishment and survivorship but did not see competition because biomass was not affected. There are also differences in opinions on the operational definition, i.e. how to measure competition, and



accordingly about the terms competitive ability, competitive superiority and competitive success. Some measure the competitive ability in terms of their ability to reduce the biomass of the target species (Gaudet & Keddy, 1988) whereas according to Tilman (1987), a species is "a superior competitor for a particular suite of environmental conditions if . . . it displaces another species" which means that competition is to be examined at all phases of the lifecycle.

Our present knowledge of competition among aquatic plants is not sufficient to answer most of these questions. We will therefore restrict our discussion to a few comments only.

One of the main areas of contention between Grime (1979) and Tilman (1987, 1988) is the competitive ability of species vis-a-vis different resources for which they may compete. According to Grime's 'unified concept of competitive ability' all species can be arranged along a gradient of competitive ability irrespective of the resource factor. On the other hand, according to Tilman's resource competition theory, the species are differentiated in their competitive abilities for different resources. Gaudet and Keddy (1988) indeed arranged 44 wetland species in order of their increasing competitive ability. Under standardized experimental conditions and using a phytometer to assess the competitive ability, they observed that biomass explains 63% variability in competitive ability, whereas plant height, canopy diameter, canopy area and leaf shape explained most of the residual variation. The use of biomass as a plant trait indicating competitive ability is however questionable. Many aquatics of similar growth form will have a similar biomass range. Do we expect that different species of duckweeds or cattails will have similar competitive abilities? McCreary (1991) has also observed that biomass is not a suitable parameter. Some studies on macrophytes tend to support the view of Tilman that the success of a species depends upon the limiting resource. For example, *Lemna trisulca* is a superior competitor for nutrients over *L. minor* which is better competitor for light (see p. 162).

According to Tilman (1988), the differentiation in the competitive ability of species is determined by the pattern of resource allocation to below ground and above ground parts which are related to the use of nutrient and light resources, respectively. This also implies that a species with higher competitive ability for nutrients will have lower competitive ability for light. These assumptions apparently ignore the changes in resource allocation pattern under different environmental conditions. It is well known that at low light intensities, the plants respond by increased specific leaf area (area/unit leaf weight), i.e., a plant may invest the same amount of photosynthate in producing more leaf surface providing it a competitive edge over others for light. In *Vallisneria americana*, Titus and Stephens (1983) observed increased leaf length and lesser number of rosettes in the presence of neighbours without a significant decrease in biomass. The aquatic macrophytes are particularly well known for their great phenotypic plasticity. A significant change in the photosynthate allocation pattern may change the plant's competitive ability for one resource without affecting that for the other. For example, in waterhyacinth the increase in the aboveground biomass and photosynthetic surface in response to crowding does not affect its ability to compete for nutrients despite lower resource (photosynthate) allocation to the roots.

Much emphasis has been placed in competition studies in general, and by both Tilman and Grime in particular, on nutrients and light as resources for which species compete. These studies fail to recognise the importance of non-resource variables like water depth which may influence the outcome of competition directly or modify the



nature and availability of the resources. The terrestrial plants are not constrained by the supply of carbon dioxide for photosynthesis or of oxygen to their below ground organs. The hypoxia or anoxia results in several other chemical changes in the sediments and water column (see Ponnampereuma, 1972; Wetzel, 1988) to which the aquatic plants may respond differently. The distribution of species along a gradient of non-resource variable like water depth can then be expected to result in variation in the competition intensity as discussed by Keddy (1990).

The studies on competition between species of *Typha* (Grace, 1987, 1988) illustrate the point. Grace (1990) points out that contrary to the expectation of competitive superiority (based on resource ratio hypothesis) of deep-water species (*T. domingensis*) in deeper water, the shallow-water species (*Typha latifolia*) is a superior competitor whereas the adaptation of deep-water species to water depth allows it a refuge from competition. This is described as a trade-off between adaptation to a non-resource and competition for resources (Grace, 1990). It is likely that similar tradeoffs occur in other aquatic plants to mask competition.

Despite some evidence of the importance of sediments as a source of nutrients for submerged macrophytes, all of them are able to use nutrients from the surrounding water, and many can use ammonia in place of nitrates (Wetzel, 1988). Therefore, the resource allocation pattern is not expected to influence the outcome of competition among submerged macrophytes. A nearly total shift in the allocation of resources from below ground organs to above ground shoots in submerged plants like *Hydrilla* and *Potamogeton pectinatus* may not affect their ability to utilize nutrients. Further, the competition for light and carbon dioxide appears to have been overcome by evolving different photosynthetic pathways (Bowes, 1987; Sondergaard, 1988). With the decreasing water depth, appear the emergents with increasing dependence on soil for nutrients and exhibit competition to a greater extent.

Thus, in our opinion, the presence of a non-resource variable, which also modifies the resource availability, and the peculiar adaptive features of aquatic plants, explain to a great extent the observed differences in the occurrence of competition. It seems reasonable to conclude that whereas competition may play a greater role among emergent species and those on waterlogged substrate, its importance decreases in species adapted to increasingly greater water depth.

#### ALLELOPATHY

A major problem faced by allelopathic investigations is methodological. Besides the obligation to test for the absence of resource competition, it is considered necessary to identify the allelochemical responsible for the growth inhibition (Muller, 1969). As Williamson (1990) puts it succinctly, "demonstration of resource competition rarely requires identification of the limiting resource, yet allelopathy is incredible without identification of the phytotoxin." Fuerst and Putnam (1983) suggested several steps to be taken to prove the existence of competitive and allelopathic interference. First, the existence of interference is demonstrated by identifying the symptoms, and possibly quantifying the degree of interference. In case of competition the presence of agent (competitor) is correlated with reduced utilization of the resources by the suspect, demonstrating which of the resource(s) depleted by the agent are limiting, and simulating interference from the agent by reducing the level of the resources considered responsible for the interference. In case of allelopathy, the toxin is to be

isolated, assayed and synthesised, and then its effect again tested at rates present in nature at appropriate stages of susceptible growth, and then to monitor the release, movement and uptake of the toxin possibly with the use of biosynthesis of radioactively labelled toxin. Further, the selectivity of toxin may be examined by comparing the effects on a range of species.

This is indeed a rigorous exercise, rarely carried out and almost wholly lacking so far in the studies of allelopathy among aquatic plants. Nevertheless, allelopathic interactions have been demonstrated at several levels though contradictory observations have often been made. Further, a number of allelochemicals have been isolated and identified from a variety of aquatic plants. Then, does allelopathy play some role in the structure and dynamics of aquatic plant communities? If yes, how important is it vis-a-vis competition and other environmental factors?

The answer to both these questions has to be sought by keeping in mind the nature of the aquatic environment. The concentration of the toxin is an important factor. In aquatic environments, the toxins produced by a plant would be increasingly diluted with greater volume of the waterbody, and are also likely to get dispersed into the sediments. The degradation and accumulation depend upon the aerobic or anaerobic nature of the sediments. The presence of toxins in the lake sediments observed by Dooris and Martin (1981) points to the possibility of their accumulation. It is important to note that greater potential significance has been attached to allelochemicals in drier habitats (Muller, 1966) where the toxins can not disperse with water, may degrade only slowly and hence, accumulate. It is likely that the higher osmotic concentrations obtained in drier habitats, coupled with the accumulation of toxins, may also influence the allelopathic effects by lowering germination substantially (cf. Bell, 1974). The importance of concentration is further demonstrated by the observations of Weidenheimer et al. (1989) that the allelopathic phytotoxicity decreased at higher density of the target plant i.e. sharing of the phytotoxin among many plants. This means that the allelopathic influence is density dependent and suggests that the allelopathic and competitive interactions may also affect each other. The rapid vegetative multiplication of most of the aquatic plants may also be therefore considered as a strategy to avoid the effects of phytotoxins.

Williamson (1990) suggests that in addition to the demonstration of the growth inhibition by the concerned allelochemical, the studies of allelopathy should address the mechanism of natural selection for production of allelochemical. Why has allelopathy evolved in some cases of resource competition but not others and what conditions other than resource competition may lead to allelopathy. One needs to demonstrate what mechanisms exist to reduce or preclude autotoxicity.

The studies on allelopathy among aquatic plants are still in their infancy and it is not possible to answer the questions related to evolution of allelopathy. The absence or reduction of autotoxicity may be explained by the assumption that each species has a different threshold concentration and differs in its response to various allelochemicals. It is significant that similar groups of allelochemicals are produced by aquatic macrophytes belonging to similar growth forms but widely different taxonomic groups. Some species like water hyacinth and *Scirpus lacustris* have indeed the ability to remove allelochemicals like phenols from their surroundings (Gopal, 1987; Seidel, 1965).

However, it is noteworthy that in some plants like *Hydrilla verticillata*, both competition and allelopathy have been reported. In general, allelopathy has been

demonstrated under conditions unfavourable for maximal growth. We hypothesise that the same plant may or may not produce allelochemicals depending upon other conditions for growth. For example, Lincoln and Couvet (1989) demonstrated that the carbon supply influences the allocation of photosynthates to the production of allelochemical. Allelopathy can then be viewed as a defense strategy under suboptimal conditions. Under favourable environments the plant is able to compete with other species using its other physiological attributes (adaptation to light, photosynthetic pathways, ability to use nutrients efficiently, reproductive effort, phenological segregation, etc.). The production of allelochemicals (secondary metabolites) themselves is influenced by the environmental conditions and thus, under unfavourable conditions, the plant resorts to an alternate strategy. For example, under conditions of nutrient enrichment, phytoplankton blooms may develop taking advantage of available nutrients or the plant may get colonised by epiphytes. In such conditions, production of allelochemicals for attracting grazers or reducing plankton blooms may occur. The production of growth promoters and attractants by some macrophytes may also indirectly help the plant through mechanisms/ processes not yet understood. In sum, a species may adopt a resource competitive strategy or an allelopathic strategy against different competitors or against the same competitor under different conditions. This appears to be the case in *Eleocharis coloradoensis*.

The differences in the role of both competition and allelopathy among species occurring along a hydrological gradient (waterlogging to deep water) and the possibility of a shift in plant strategy in response to environmental conditions have important implications for the community structure and dynamics in seasonal/temporary habitats. Large water level changes and periodic drying of waterbodies may result in changes in community structure in successive years depending upon the accumulation of allelochemicals in sediments, the seed bank, growth rate and competitive ability of different species.

### VIII. Application of Competition and Allelopathy

Besides the theoretical importance of competition and allelopathy as discussed above, there is a growing interest in the practical application of these studies in the management of natural resources (e.g., forestry, agriculture) and control of plant and animal pests (Szczepanska, 1977a; Whittaker & Feeney, 1971; Yeo, 1980; Yeo & Fisher, 1970; Yeo & Thurston, 1984). Some of the more important studies only are mentioned here.

#### BIOLOGICAL CONTROL

It may be possible to control the growth of a noxious plant by introducing a plant with greater competitive ability or with allelopathic potential (Numata, 1982; Putnam, 1988; Yeo, 1972, 1976). Another possibility lies in the use of allelopathic substances artificially introduced into the waterbody infested by the weeds. Mehta and Sharma (1975) indeed demonstrated by field studies that *Typha angustata* could be effectively controlled by introducing *Brachiaria mutica*. Since Szczepanski (1977) suggested that allelopathy can play an important role in the biological control of aquatic weeds, much of the work on allelopathic potential of aquatic plants is directed towards this goal (Elakovich, 1989; Elakovich & Wooten 1989a). The duckweed (*Lemna minor*)

bioassay has been developed with this possibility in mind though it is likely that a substance toxic to *Lemna minor* may not affect other aquatic plants. The search for the allelopathic compounds is being pursued also in the sediments where they may accumulate from different sources (Dooris & Martin, 1981, 1985). More recently, the allelopathic potential of terrestrial plants like *Lantana camara* to control water hyacinth has also been reported (Saxena, 1992).

#### AGRICULTURE

Rice is one of the major crops throughout the tropics and feeds more than half of humankind. Most of the varieties of rice are grown as a wetland crop where numerous other aquatic and marsh plants are commonly associated. There are also other aquatic crops of importance, e.g., jute and taro. The available studies show that not only the weeds in paddy fields compete with rice for nutrients but some are allelopathic to it. Further, the rice itself appears to be allelopathic to other crops. The decomposition products of straw are particularly highly toxic with implications for the cultivation of other crops after paddy is harvested, and also for the paddy itself (Chou, 1990, Chou & Chiou, 1979; Chou et al., 1981).

There is sufficient evidence to conclude that many aquatic plants adversely affect the germination and seedling growth of a variety of crop plants. Therefore, the use of these plants as mulch has to be viewed with caution.

### IX. Conclusions

Our present state of understanding of competition and allelopathy among aquatic plant communities is too meagre and fragmentary. The available information suggests that the aquatic environment has a significant impact on the processes of competition and allelopathy, and that the aquatic plants of various growth forms differ greatly among themselves in their responses and adaptations to competition and allelopathy. Both extensive and intensive studies are required to explain the role of these interactions in aquatic communities and their practical significance, if any.

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### XI. Literature Cited

- Abu Gideiri, Y.B. & A.M. Yousif. 1974. The influence of *Eichhornia crassipes* Solms. on planktonic development in the White Nile. Arch. Hydrobiol. **74**: 463–467.
- Achhireddy, N.R. & Megh Singh. 1984. Allelopathic effects of Lantana (*Lantana camara*) on milkweedvine (*Morrenia odorata*). Weed Sci. **32**: 757–761.
- Achmatowicz, O. & Z. Bellen. 1962. Tetrahedron Lett. 1121.
- Agami, M. & K.R. Reddy. 1989. Inter-relationships between *Salvinia rotundifolia* and *Spirodela*

- polyrhiza* at various interaction stages. *J. Aquatic Pl. Managem.* **27**: 96–102.
- & ———. 1990. Competition for space between *Eichhornia crassipes* (Mart.) Solms. and *Pistia stratiotes* L. cultured in nutrient enriched water. *Aquatic Bot.* **38**: 195–208.
- & ———. 1991. Inter-relationship between *Eichhornia crassipes* (Mart.) Solms and *Hydrocotyle umbellata* L. *Aquatic Bot.* **39**: 147–157.
- & Y. Waisel. 1985. Inter-relationships between *Najas marina* L. and three other species of aquatic macrophytes. *Hydrobiologia* **126**: 169–173.
- Akhtar, S. 1978. Some molluscs associated with water hyacinth. *Pakistan J. Sci.* **30**: 20–22.
- Aliotta, G., N. Della Greca, P. Monaco, G. Pinto, A. Pollio & L. Previtera. 1990. In vitro algal growth inhibition by phytotoxins of *Typha latifolia* L. *J. Chem. Ecol.* **16**: 2637–2646.
- Allanson, B.R. 1973. The fine structure of the periphyton of *Chara* sp. and *Potamogeton natans* from Wytham pond, Oxford and its significance to the macrophyte periphyton metabolic model of R.G. Wetzel and H.L. Allen. *Freshwater Biol.* **3**: 535–541.
- Allen, E.D. & D.H.N. Spence. 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytol.* **87**: 269–283.
- Allen, H.L. 1971. Primary productivity, chemo-organography and nutritional interactions of epiphytic algae and bacteria on macrophytes in a lake. *Ecol. Monogr.* **41**: 97–127.
- Alsaadawi, I.S., E.L. Rice & T.K.B. Karns. 1983. Allelopathic effects of *Polygonum aviculare* L. III. Isolation, characterization and biological phytotoxins other than phenols. *J. Chem. Ecol.* **9**(6): 761–773.
- Anderson, L.W.J. 1985. Use of bioassays for allelochemicals in aquatic plants. Pages 351–370, in A.G. Thompson (ed.) *The chemistry of allelopathy*. ACS Symposium series 268. American Chemical Society, Washington, D.C.
- Anderson, M.R. & J. Kalf. 1986. Regulation of submersed aquatic plant distribution in a uniform area of a weedbed. *J. Ecol.* **74**: 953–961.
- Anthoni, U. & A. Christophersen. 1982. Synthesis of 4-methylthio-1,2-dithiolane and 5-methylthio-1,2,3-Trithiane. Two naturally occurring bioactive compounds. *Tetrahedron* **38**(15): 2425–2427.
- , C. Christophersen, J.O. Madsen, S. Wium Andersen & N. Jacobsen. 1980. Biologically active sulphur compounds from the green alga *Chara globularis*. *Phytochemistry* **19**: 1228–1229.
- Ashton, F.M. & S.R. Bissel. 1987. Influence of temperature and light on dwarf spikerush and slender spikerush growth. *J. Aquatic Pl. Managem.* **25**: 4–7.
- , J.M. Ditomasco & L.W.J. Anderson. 1985. Spikerush (*Eleocharis* spp.): A source of allelopathics for the control of undesirable aquatic weeds. *J. Aquatic Pl. Managem.* **22**: 52–56.
- Austin, M.P. 1990. Community theory and competition in vegetation. Pages 215–238, in J.B. Grace & D. Tilman (eds.) *Perspectives on plant competition*. Academic Press, San Diego, CA, USA.
- Bachmann, A. 1921. A programme to be carried out in Familla against Anopheles and their larvae (in Spanish). *An. Dept Nac. Higiene, Buenos Aires* **27**: 117–137.
- Barko, J.W. & R.M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. *Freshwater Biol.* **10**: 229–238.
- & ———. 1981. Comparative influence of light and temperature on the growth of selected submersed macrophytes. *Ecol. Monogr.* **51**: 219–235.
- Bartrop, J. & D.F. Martin. 1983. Evidence for photodynamic action by a naturally occurring *Hydrilla* growth inhibitor. *J. Environm. Sci. Health, A.* **18**: 29–36.
- Bate-Smith, E.C. 1968. *Phytochemistry* **7**: 459. (cited from McClure, 1970).
- Begon, M., J.L. Harper & C.R. Townsend. 1986. *Ecology: Individuals, populations and communities*. Blackwells, Oxford, U.K.
- Bell, David J. 1974. The influence of osmotic pressure in tests for allelopathy. *Trans. Illinois State Acad. Sci.* **67**: 312–317.
- Bell, D.T. & C.H. Muller. 1973. Dominance of California annual grasslands by *Brassica nigra*. *Amer. Midl. Naturalist* **90**: 277–299.
- Bel'tyukova, K.C. & L.T. Pastushenko. 1963. Antibiotic effect of nupharine on pathogenic bacteria in vitro and in vivo. *Mikrobiol. Zh. Akad. Nauk. Ukr. RSR* **25**: 36. *Chem. Abstr.* **59**: 5536f.
- Best, E.P.H. 1988. The phytosociological approach to the description and classification of aquatic

- macrophytic vegetation. Pages 155–182, in J.J. Symoens (ed.) *Vegetation of inland waters. Handbook of vegetation science 15/1*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Bhanja, A., R.K. Mukherjee, N.K. Roy, S. Banerjee, P.K. Sircar & S.M. Sircar.** 1968. Isolation and identification of growth substances in the root of water hyacinth (*Eichhornia crassipes* (Mart.) Solms.). *Proc. int. symp. plant growth substances*: 47–56. Botany Dept., University Calcutta, Calcutta, India.
- Björndahl, G.** 1983. Structure and biomass of *Phragmites* stands. Ph.D. thesis, University of Goteborg, Sweden.
- Blindlow, I.** 1987. The composition and density of epiphyton on several species of submerged macrophytes- the neutral substrate hypothesis tested. *Aquatic Bot.* **29**: 157–168.
- Bonaseria, J., J. Lynch & M.A. Leck.** 1979. Comparison of the allelopathic potential of four marsh species. *Bull. Torrey Bot. Club* **106**: 217–222.
- Bornkamm, R.** 1970. Über den Einfluss der Konkurrenz auf die Substanzproduktion und den N-gehalt der Wettbewerbspartner. *Flora* **159**: 84–104.
- Bowes, G.** 1987. Aquatic plant photosynthesis: strategies that enhance carbon gain. Pages 79–98, in R.M.M. Crawford (ed.) *Plant life in aquatic and amphibious habitats*. Blackwells, Oxford, U.K..
- Brammer, E.S.** 1979. Exclusion of phytoplankton in the proximity of dominant water soldier (*Stratiotes aloides*). *Freshwater Biol.* **9**: 233–249.
- Brönmark, C.** 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* **45**: 26–30.
- . 1989. Interactions between epiphytes, macrophytes, and freshwater snails: a review. *J. Mollusc. Stud.* **55**: 299–311.
- Bulthuis, D.A. & Wm. J. Woelkerling.** 1983. Biomass accumulation and shading effects of epiphytes of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquatic Bot.* **16**: 137–148.
- Burkholder, J.A. & R.G. Wetzel.** 1990. Alkaline phosphatase and algal biomass on natural and artificial plants in an oligotrophic lake: Reevaluation of the role of macrophytes as a phosphorus source for epiphytes. *Limnol. & Oceanogr.* **35**: 432–443.
- Buttery, B.R. & J.M. Lambert.** 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. 1. The competition mechanism. *J. Ecol.* **53**: 163–182.
- Carignan, & J. Kalff.** 1982. Phosphorus release by submersed macrophytes: Significance to epiphyton and phytoplankton. *Limnol. & Oceanogr.* **27**: 419–427.
- Carter, M.F. & J.C. Grace.** 1986. Relative effects of *Justicia americana* litter on germination, seedlings and established plants of *Polygonum lapathifolium*. *Aquatic Bot.* **23**: 341–349.
- Cattaneo, A.** 1983. Grazing on epiphytes. *Limnol. & Oceanogr.* **28**: 124–132.
- Center, T.D. & N.R. Spencer.** 1981. The phenology and growth of water hyacinth (*Eichhornia crassipes* (Mart.) Solms.) in a eutrophic north-central Florida lake. *Aquatic Bot.* **10**: 1–32.
- Chadwick, M.J. & M. Obeid.** 1966. A comparative study of the growth of *Eichhornia crassipes* Solms. and *Pistia stratiotes* L. in water culture. *J. Ecol.* **54**: 563–575.
- Chambers, P.A.** 1987. Light and nutrients in the control of aquatic plant community structure. II. In situ observations. *J. Ecol.* **75**: 621–628.
- & **J. Kalff.** 1987. Light and nutrients in the control of aquatic plant community structure. I. In situ experiments. *J. Ecol.* **75**: 611–619.
- & **E. E. Prepas.** 1990. Competition and coexistence in submerged aquatic plant communities: the effects of species interactions versus abiotic factors. *Freshwater Biol.* **23**: 541–550.
- Cheng, T.S. & D.N. Riemer.** 1988. Allelopathy in threesquare burreed (*Sparganium americanum*) and American eelgrass (*Vallisneria spiralis*). *J. Aquatic Pl. Managem.* **26**: 50–55.
- & ———. 1989. Characterization of allelochemicals in American eelgrass. *J. Aquatic Pl. Managem.* **27**: 84–89.
- Cherrett, J.M. (ed.)** 1989. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwells, Oxford, U.K.
- Chou, C.H.** 1980. Allelopathic researches in the subtropical vegetation in Taiwan. *Comp. Physiol. Ecol.* **5**: 222–234.



- . 1990. The role of allelopathy in agroecosystems: Studies from tropical Taiwan. Pages 104–121, in *Agroecology. Ecological studies* 78. Springer Verlag, Berlin, Germany.
- & **S.-J. Chiou**. 1979. Autointoxication mechanism of *Oryza sativa*. II. Effects of culture treatments on the chemical nature of paddy soil and on rice productivity. *J. Chem. Ecol.* **5**: 839–859.
- , **Y.-C. Chiang & H.H. Cheng**. 1981. Autointoxication mechanism of *Oryza sativa*. III. Effect of temperature on phytotoxin production during rice straw decomposition in soil. *J. Chem. Ecol.* **7**: 741–752.
- , **M.L. Lee & H.I. Okaa**. 1984. Possible allelopathic interaction between *Oryza perennis* and *Leersia hexandra*. *Bot. Bull. Acad. Sin.* **25**: 1–19.
- , **S.Y. Hwang, C.I. Peng, Y.C. Wang, F.H. Hsu & N.J. Chung**. 1987. The selective allelopathic interaction of a pasture forest intercropping system in Taiwan. *Pl. & Soil* **98**: 31–41.
- Clatworthy, J.N. & J.L. Harper**. 1962. The comparative biology of closely related species living in the same area. V. Inter and intraspecific interference within cultures of *Lemna* sp. and *Salvinia natans*. *J. Exp. Bot.* **13**: 307–324.
- Cleland, C.F. & O. Tanaka**. 1982. Influence of plant growth substances and salicylic acid on flowering and growth in the Lemnaceae (duckweeds). *Aquatic Bot.* **13**: 3–20.
- Clements, F.E.** 1904. The development and structure of vegetation. *Bot. Surv. Nebraska* **7**: 5–175.
- . 1916. *Plant Succession. Analysis of the development of vegetation*. Carnegie Inst. Washington Publ. 242. Washington, D.C.
- Clough, K.S., T.A. DeBusk & K.R. Reddy**. 1987. Model water hyacinth and pennywort systems for the secondary treatment of domestic wastewater. Pages 775–781, in K.R. Reddy & W.H. Smith (eds) *Aquatic plants for water treatment and resource recovery*. Magnolia Publishing, Orlando, FL., USA.
- Connell, J.H.** 1990. Apparent versus “real” competition in plants. Pages 9–26, in J.B. Grace & D. Tilman (eds) *Perspectives on plant competition*. Academic Press, San Diego, USA.
- Connor, E.F. & D. Simberloff**. 1979. The assembly of species communities: chance or competition. *Ecology* **60**: 1132–1140.
- & ———. 1983. Interspecific competition and species co-occurrence patterns on islands: use of null models and the evaluation of evidence. *Oikos* **41**: 455–465.
- Crawford, S.A.** 1979. Farm pond restoration using *Chara vulgaris* vegetation. *Hydrobiologia* **62**: 17–31.
- Dale, D.** 1992. An allomone in rice plant against stem borer. Pages 171–174, in P. Tauro & S.S. Narwal (eds) *Proc. first nat. symp. allelopathy in agroecosystems*. Indian Society of Allelopathy, Haryana Agric. University, Hissar, India.
- Dale, H.M.** 1986. Temperature and light: the determining factors in maximum depth distribution of aquatic macrophytes in Ontario, Canada. *Hydrobiologia* **133**: 73–77.
- Darwin, C.** 1859. *The Origin of Species by Means of Natural Selection*. Penguin Books, Harmondsworth. (Reprinted ed. 1968).
- Dazo, B.C., N.G. Hairston & I.K. Dawood**. 1966. The ecology of *Bulinus truncatus* and *Biomphalaria alexandrina* and its implications for the control of Bilharziasis in the Egypt 49 Project Area. *Bull. WHO* **35**: 339–356.
- Della Greca, M., L. Mangoni, A. Molinaro, P. Monaco & L. Previtera**. 1990. (20S)-4-methyl-24-methylenecholest-7-en-3-ol, an allelopathic sterol from *Typha latifolia*. *Phytochemistry* **29**(6): 1797–1798.
- DeBusk, T.A., J.H. Ryther, M.D. Hanisak & L.D. Williams**. 1981. Effects of seasonality and plant density on the productivity of some freshwater macrophytes. *Aquatic Bot.* **10**: 133–142.
- DeSilva, M.P., M.A. Pemadasa, I. Balasooriya, S.I. Abeygunawardena & C. Nanayakkara**. 1984. A preliminary study of the interaction between *Eichhornia crassipes* (Mart.) Solms. and *Salvinia molesta* Mitchell. Pages 298–303, in G. Thyagarajan (ed) *Proc. int. conf. water hyacinth*. United Nations Environment Programme, Nairobi.
- DeWit, C.T.** 1960. On competition. *Verslagen Landbouwk. Onderz.* **66**: 1–82.
- Dey, B.** 1982. Studies on weed biology of *Echinochloa crusgalli* (L.) Beauv. and its competitive relationships with rice. Ph.D. thesis, North Eastern Hill University, Shillong, India.

- Dhillon, M.S., M.S. Mulla & Yin-Shen Hwang.** 1982. Allelochemicals produced by the hydrophyte *Myriophyllum spicatum* affecting mosquitoes and midges. *J. Chem. Ecol.* **8**(2): 517–526.
- Docauer, D.M.** 1983. A nutrient basis for the distribution of the Lemnaceae. Ph.D. thesis, University of Michigan, Ann Arbor, MI.
- Dooris, G.M., P.M. Dooris & D.F. Martin.** 1988. Effect of a naturally occurring growth inhibitor on the ultrastructure of hydrilla. *J. Aquatic Pl. Managem.* **26**: 72–73.
- Dooris, P.M. & D.F. Martin.** 1981. Growth inhibition of *Hydrilla verticillata* by selected lake sediment extracts. *Water Res. Bull.* **16**: 112–117.
- & ———. 1982. Control of macrophytic growth by naturally produced substances. Pages 61–75, in E.O. Gangstad (ed.) *Weed control methods for recreation facilities management*. CRC Press, Boca Raton, FL., USA.
- & ———. 1985. Naturally occurring substances that inhibit the growth of *Hydrilla verticillata*. Pages 381–386, in A.C. Thompson (ed.) *The chemistry of allelopathy*. ACS Symposium series 268. American Chemical Society, Washington, D.C.
- , **W.S. Silver & D.F. Martin.** 1982. Effect of *Hydrilla verticillata* growth inhibiting extracts upon the growth of *Scenedesmus obliquus* (an alga). *J. Environm. Sci. Health, A.* **17**: 639–646.
- Dorgelo, J. & K. Koning.** 1980. Avoidance of macrophytes and additional notes on avoidance of the shore by *Acanthodiptomus denticornis* (Wierzejski 1887) from lake Pavin (Auvergne, France). *Hydrobiol. Bull.* **14**: 196–208.
- Drobot'ko, V.G., E. Ya. Rashba, B.E. Aizenman, S.I. Zelepukha, S.I. Novikova & M.B. Kaganskaya.** 1958. Antimicrobial activity of alkaloids obtained from *Valeriana officinalis*, *Chelidonium majus*, *Nuphar luteum* and *Asarum europaeum*. *Antibiotiki* 1958: 22; *Chem. Abstr.* **53**: 12589d.
- Drost, D.C. & J.D. Doll.** 1980. The allelopathic effect of yellow nutsedge (*Cyperus esculentus*) on corn (*Zea mays*) and soybeans (*Glycine max*). *Weed Sci.* **28**: 229–233.
- Einhellig, F.A., G.R. Leather & L.L. Hobbs.** 1985. Use of *Lemna minor* L. as a bioassay in allelopathy. *J. Chem. Ecol.* **11**: 65–72.
- Elakovich, S.D.** 1989. Allelopathic aquatic plants for aquatic weed management. *Biol. Pl.* **31**(6): 479–486.
- & **J.W. Wooten.** 1987. An examination of the phytotoxicity of the water shield, *Brasenia schreberi*. *J. Chem. Ecol.* **13**: 1935–1940.
- & ———. 1989a. Allelopathic aquatic plants for aquatic plant management: a feasibility study. *Aquatic Plant Control Program Tech. Rept A–89–2*. U.S. Dept of the Army, Army Corps of Engineers, Washington, D.C.
- & ———. 1989b. Allelopathic potential of sixteen aquatic and wetland plants. *J. Aquatic Pl. Managem.* **27**: 78–84.
- & ———. 1991. Allelopathic potential of *Nuphar lutea* (L.) Sibth. & Sm. (Nymphaeaceae). *J. Chem. Ecol.* **17**: 701–714.
- El-Ghazal, R.A.K. & D.N. Reimer.** 1986. Germination suppression by extracts of aquatic plants. *J. Aquatic Pl. Managem.* **24**: 76–79.
- Eminson, D. & B. Moss.** 1980. The composition and ecology of periphyton communities in freshwaters. 1. The influence of host type and external environment on community composition. *Brit. Phycol. J.* **15**: 429–446.
- Evenari, M.** 1949. Germination inhibitors. *Bot. Rev.* **15**: 153–194.
- Feeney, P.P.** 1976. Plant apparency and chemical defense. *Phytochemistry* **10**: 1–40.
- Feoli, E. & L. Orloci** (eds). 1991. Computer assisted vegetation analysis. *Handbook of vegetation science* 11. Kluwer Academic Publishers, Dordrecht.
- Fitzgerald, G.P.** 1969. Some factors in competition or antagonism among bacteria algae and aquatic weeds. *J. Phycol.* **5**: 351–359.
- Forsberg, C., S. Kleiven & T. Willen.** 1990. Absence of allelopathic effects of *Chara* on phytoplankton in situ. *Aquatic Bot.* **38**: 289–294.

- Frank, P.A. & N. Dechoretz.** 1980. Allelopathy in dwarf spikerush (*Eleocharis coloradoensis*). *Weed Sci.* **28**: 499–505.
- Fuerst, E.P. & A.R. Putnam.** 1983. Separating the competitive and allelopathic components of interference. *J. Chem. Ecol.* **9**: 937–944.
- Gaudet, C.L. & P.A. Keddy.** 1988. A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242–243.
- Gaveskaya, N.S.** 1969. The role of higher aquatic plants in the nutrition of the animals of freshwater basins. (Ed. by K.H. Mann, translated from Russian by D.G. Maitland Muller). National Lending Library, Boston Spa. U.K.
- Gay, P.A.** 1960. Ecological studies of *Eichhornia crassipes* Solms. in the Sudan. I. Analysis of spread in the Nile. *J. Ecol.* **48**: 183–191.
- George, K.** 1976. Studies on the chemical control of some important aquatic weeds of Kerala, *Salvinia*, *Ludwigia* and *Cyperus*. Pages 255–262, in C.K. Varshney & J. Rzoska (eds.) *Aquatic weeds in south east Asia*. W. Junk, The Hague.
- Gessner, F.** 1955. *Hydrobotanik. Die physiologischen Grundlagen der Pflanzenverbreitung im Wasser. I. Energiehaushalt.* VEB Deutscher Verlag der Wissenschaften, Berlin, Germany.
- . 1959. *Hydrobotanik. Die physiologischen Grundlagen der Pflanzenverbreitung im Wasser. II. Stoffhaushalt.* VEB Deutscher Verlag der Wissenschaften, Berlin, Germany.
- Gibbs, R.D.** 1974. *Chemotaxonomy of flowering plants.* McGill and Queens University Press, Montreal, Canada.
- Godmaire, H. & C. Nalewajko.** 1990. Structure and development of secretory trichomes on *Myriophyllum spicatum* L. *Aquatic Bot.* **37**: 99–122.
- Gopal, B.** 1987. *Water Hyacinth. Aquatic Plant Studies 1.* Elsevier Science Publishers, Amsterdam.
- Goulder, R.** 1969. Interactions between the rates of production of a freshwater macrophyte and phytoplankton in a pond. *Oikos* **20**: 300–309.
- Grace, J.B.** 1983. Autotoxic inhibition of seed germination by *Typha latifolia*: an evaluation. *Oecologia*. **59**: 366–369.
- . 1987. The impact of pre-emption on the zonation of *Typha* species along lakeshores. *Ecol. Monogr.* **57**(4): 283–303.
- . 1988. The effect of nutrient additions on mixtures of *Typha latifolia* and *Typha domingensis* Pers. along a water depth gradient. *Aquatic Bot.* **31**: 83–92.
- . 1990. On the relationship between plant traits and competitive ability. Pages 51–65, in J.B. Grace & D. Tilman (eds) *Perspectives on plant competition.* Academic Press, San Diego, CA, USA.
- & **D. Tilman** (eds). 1990. *Perspectives on Plant Competition.* Academic Press, San Diego, CA, USA.
- & **R.G. Wetzel.** 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies. *Amer. Naturalist* **118**: 463–474.
- Graneli, W.** 1987. Shoot density regulation in stands of reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **27**: 211–222.
- Grime, J.P.** 1979. *Plant strategies and vegetation processes.* John Wiley, Chichester, U.K.
- Gross, E.M., C.P. Wolk & F. Jüttner.** 1991. Fischerellin, a new allelochemical from the freshwater cyanobacterium *Fischerella muscicola*. *J. Phycol.* **27**: 686–692.
- Guseva, K.A. & S.P. Goncharova.** 1965. O vliianii vysshei vodnoi rastitel 'nosti na razvitie planktonnykh sinezelenykh vodoroslei. *Ekologiya i Fiziologiya Sinezelenykh Vodoroslei*: 230–234. Leningrad.
- Hairston, N.G., F.E. Smith & L.G. Slobodkin.** 1960. Community structure, population control and competition. *Amer. Naturalist* **94**: 421–425.
- Haller, W.T.** 1974. Photosynthetic characteristics of the submersed aquatic plants *Hydrilla*, Southern Naiad and *Vallisneria*. Ph.D. dissertation, University of Florida, Gainesville, FL, USA.
- & **D.L. Sutton.** 1975. Community structure and competition between the aquatic weed *Hydrilla verticillata* and *Vallisneria neotropicalis*. *Hyacinth Control J.* **13**: 48–50.
- Harborne, J.B.** 1977. *Introduction to ecological biochemistry.* Academic Press, London.

- Harper, J.L.** 1961. Approaches to the study of plant competition. Pages 1–39, in F.L. Milthorpe (ed.) *Mechanisms in biological competition*. Society for Experimental Biology, Cambridge University Press, Cambridge.
- . 1964. The nature and sequence of interference amongst plants. *Proc. XI Int. Congr. Genet.* **2**: 465–482.
- . 1977. *Population Biology of Plants*. Academic Press, New York.
- Harrison, P.G. & C. Durance.** 1985. Reductions in photosynthetic carbon uptake in epiphytic diatoms by water soluble extracts of leaves of *Zostera marina*. *Mar. Biol.* **90**: 117–119.
- Hartog, C. den & S. Segal.** 1964. A new classification of the water plant communities. *Acta Bot. Néerl.* **13**: 367–393.
- & **G. van der Velde.** 1988. Structural aspects of aquatic plant communities. Pages 113–154, in J.J. Symoens (ed.) *Vegetation of inland waters. Handbook of vegetation science 15/1*. Kluwer Academic Publishers, Dordrecht.
- Hasler, A.D. & E. Jones.** 1949. Demonstration of antagonistic action of large aquatic plants on algae and rotifers. *Ecology* **30**: 359–364.
- Hejny, S.** 1960. Ökologische Charakteristik der Wasser- und Sumpfpflanzen in den slowakischen Tiefebene. *Slovak. Akad. Wiss., Bratislava*.
- . 1971. The dynamic characteristics of littoral vegetation with respect to changes of water level. *Hydrobiologia* **12**: 71–85.
- Hogeweg, P. & A.L. Brenkert-van Riet.** 1969. Structure of aquatic vegetation: a comparison of aquatic vegetation in India, the Netherlands and Czechoslovakia. *Trop. Ecol.* **10**: 139–162.
- Holm, L.** 1969. Chemical interaction between plants on agricultural lands. *Down to Earth* **25**: 16–22.
- Hootsmans, M.J.M. & J.E. Vermaat.** 1985. The effects of periphyton grazing by three epifaunal species on the growth of *Zostera marina*. L. under experimental conditions. *Aquatic Bot.* **22**: 83–88.
- Horecka, M.** 1991. The significant role of *Chara hispida* grown in water regime of a gravel pit lake at Senec. *Arch. Protistenkd.* **139**: 275–278.
- Howard, R.K.** 1982. Impact of activities of epibenthic amphipods on surface-fouling of eelgrass leaves. *Aquatic Bot.* **14**: 91–97.
- & **F.T. Short.** 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. *Aquatic Bot.* **24**: 287–302.
- Howard-Williams, C.** 1978. Growth and production of aquatic macrophytes in a South African temperate saline lake. *Verh. Int. Verein. Limnol.* **20**: 1153–1158.
- . 1981. Studies on the ability of a *Potamogeton pectinatus* community to remove dissolved nitrogen and phosphorus compounds from lake water. *J. Appl. Ecol.* **18**: 619–637.
- & **B.R. Allanson.** 1981. Phosphorus cycling in a *Potamogeton pectinatus* L. bed. *Oecologia*. **49**: 56–66.
- Hutchinson, G.E.** 1970. The chemical ecology of three species of *Myriophyllum* (Angiospermae, Haloragaceae). *Limn. & Oceanogr.* **15**: 1–5.
- . 1975. A treatise on limnology. Vol. III. *Limnological botany*. J. Wiley & Sons, Chichester, U.K.
- Iakawa, M., V.M. Thomas, L.J. Buckley & J.J. Uebel.** 1973. *J. Phycol.* **9**: 302–305. (cited from Wium-Anderson et al., 1983).
- Ikusima, I.** 1955. Growth of duckweed populations as related to frond density. *Physiol. Ecol. Japan* **6**: 69–81. (in Japanese).
- , **K. Shinozaki & T. Kira.** 1955. Intraspecific competition among higher plants. III. Growth of duckweed, with a theoretical consideration of the C-D effect. *J. Inst. Polytechn. Osaka City Univ. Ser. Biol.* **D6**: 107–119.
- Iswaran, V. & A. Sen.** 1973. Influence of extract of water hyacinth (*Eichhornia crassipes*) on the yield of brinjal (*Solanum melongena*) var. Pusa Kranti. *Sci. & Cult.* **39**: 394–395.
- Izac, R., D. Stierle & J. Sims.** 1982. Phytochemistry **21**: 229. (cited from Wium-Anderson et al., 1983).
- Jacobsen, N. & L.E.K. Pedersen.** 1983. Synthesis and insecticidal properties of Propane–1, 3-dithiol (Analogues of the insecticidal derivatives of Dithiolane & Trithiane from the alga *Chara globularis* Thuillier). *Pestic. Sci.* **14**: 90–97.

- Jain, R., Megh Singh & D.J. Dezman.** 1989. Qualitative and quantitative characterization of phenolic compounds from Lantana (*Lantana camara*) leaves. *Weed Sci.* **17**: 302–307.
- Jangaard, N.O., M.M. Sckeri, & R.H. Schieferstein.** 1971. The role of phenolics and abscisic acid in nutsedge tuber dormancy. *Weed Sci.* **19**: 17–20.
- Jasnowski, M.** 1975. Torfowiska i tereny bagienne W Polsce. Pages 356–390. in N.J. Kac (ed.) *Bagna kuli zlemskiej*. PWN, Warszawa, Poland.
- Johansson, M.E. & P.A. Keddy.** 1991. Intensity and asymmetry of competition between pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos* **60**: 27–34.
- Johnston, D.L., D.L. Sutton, V.V. Vandiver Jr, & K.A. Langeland.** 1983. Replacement of *Hydrilla verticillata* by other aquatic plants in a pond with emphasis on growth of American lotus (*Nelumbo lutea*). *J. Aquatic Pl. Managem.* **21**: 41–43.
- Jones, R.C., K. Walti & M.S. Adams.** 1983. Phytoplankton as a factor in decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra Wisconsin. *Hydrobiologia* **107**: 213–219.
- Junk, W.J.** 1977. The invertebrate fauna of the floating vegetation of Bung Borapet, a reservoir in central Thailand. *Hydrobiologia* **53**: 229–238.
- Jupp, B.P. & D.H.N. Spence.** 1977. Limitations on macrophytes in a eutrophic lake Loch leven 1. Effects of phytoplankton. *J. Ecol.* **65**: 175–186.
- Jurd, L., T.A. Geissman & M.K. Seikel.** 1957. *Arch. Biochem. Biophys.* **67**: 284. (cited from McClure, 1970).
- Jüttner, F.** 1981. Biologically active compounds released during algal blooms. *Verh. Int. Verein. Limnol.* **21**: 227–230.
- Kaul, V. & U. Bakaya.** 1976. The noxious floating lemnid-Salvinia aquatic weed complex in Kashmir. Pages 188–192, in C.K. Varshney & J. Rzoska (eds) *Aquatic weeds in south east Asia*. W. Junk, The Hague.
- Kautsky, L.** 1991. In situ experiments on interrelationships between six brackish macrophyte species. *Aquatic Bot.* **39**: 159–172.
- Keating, K.J.** 1977. Allelopathic influence on blue green bloom sequence in a eutrophic lake. *Science* **196**: 885–887.
- Keddy, P.A.** 1976. Lakes as islands: the distributional ecology of two aquatic plants, *Lemna minor* L. and *L. trisulca* L. *Ecology* **57**: 353–359.
- . 1989. *Competition*. Chapman & Hall, London.
- . 1990. Competitive hierarchies and centrifugal organization in plant communities. Pages 265–290, in J.B. Grace & D. Tilman (eds.) *Perspectives on plant competition*. Academic Press, San Diego, CA, USA.
- Keeley, J.E.** 1981. *Isoetes howellii*: a submerged aquatic CAM plant? *Amer. J. Bot.* **68**: 420–424.
- Kirpenko, N.I.** 1986. Phytopathic properties of the toxin of bluegreen algae. *Gidrobiol. Zhurn.* **22**(1): 48–50.
- Kleiven, S.W. & W. Szczepanska.** 1988. The effects of extracts of *Chara tomentosa* and two other aquatic macrophytes on seed germination. *Aquatic Bot.* **32**: 193–198.
- Kogan, S.I. & G.A. Chinnova.** 1972. Relations between *Ceratophyllum demersum* (L.) and some blue-green algae. *Hydrobiol. J. (USSR, Translation Ser.)* **8**: 14–25.
- Kohli, R.K., K. Kaur, P. Chaudhry, A. Kumari & D.B. Saxena.** 1987. Negative aspects of Eucalyptus farming. Pages 225–233, in P.K. Khosla & D.K. Khurana (eds.) *Agroforestry for rural needs*. Indian Society of Tree Scientists, Solan, India.
- Krishnamoorthi, K.P., S. Shende & M.K. Abdulappa.** 1968. On a collection of some molluscs (bivalves and gastropods) from some water bodies of Nagpur with ecological notes. *Environm. Health* **10**: 43–50.
- Kulshreshtha, M.** 1981. Allelochemic influence of some aquatic macrophytes. *Acta Limnol. Indica* **1**: 35–37.
- & **B. Gopal.** 1983. Allelopathic influence of *Hydrilla verticillata* (L.F.) Royle on the distribution of *Ceratophyllum* species. *Aquatic Bot.* **16**: 207–209.

- Kushari, D.P.** 1987. Effect of leaf leachates of neem and shirish on the biomass production of *Azolla pinnata*. Int. Rice Res. Newslett. **12**: 34.
- LaLonde, R.T., C.D. Morris, C.F. Wong, L.C. Gardner, D.J. Eckert, D.R. King & R.H. Zimmerman.** 1979. Response of *Aedes triseriatus* larvae to fatty acids of *Cladophora*. J. Chem. Ecol. **5**: 371–381.
- Landolt, E.** 1957. Physiologische und ökologische Untersuchungen an Lemnaceen. Ber. Schweiz. Bot. Gesell. **67**: 271–410.
- . 1986. Biosystematic investigations in the family of duckweeds (Lemnaceae). Vol. 2. The family of Lemnaceae- a monographic study. Vol. 1. Veröffent. Geobot. Inst. Eidg. Hochschule, Stift. Rübel, Zurich 71.
- & **R. Kandeler.** 1987. Biosystematic investigations in the family of duckweeds (Lemnaceae). Vol. 4. The family of Lemnaceae- a monographic study. Vol. 2. Veröffent. Geobot. Inst. Eidg. Hochschule, Stift. Rübel, Zurich 95.
- Law, R. & A.R. Watkinson.** 1989. Competition. Pages 243–284, in J.M. Cherrett (ed.) Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwells, Oxford, U.K..
- Leather, G.R. & F.A. Einhellig.** 1985. Mechanisms of allelopathic action in bioassay. Pages 197–205, in A.C. Thompson (ed.) The chemistry of allelopathy. ACS Symposium series 268. American Chemical Society, Washington, D.C. USA.
- & ———. 1986. Bioassay in the study of allelopathy. Pages 133–145, in A.R. Putnam and C.S. Tang (eds.) The science of allelopathy. John Wiley, New York.
- & ———. 1988. The bioassay of naturally occurring allelochemicals for phytotoxicity. J. Chem. Ecol. **14**: 1821–1828.
- Lee, H.K. & J.O. Guh.** 1982. Study on competition ability and chemical control of *Sagittaria pygmaea* Miquel- a perennial weed in paddy field. Nongsa Sihom Yongu Pogo **24**: 16–23.
- Lincoln, D.E. & D. Couvet.** 1989. The effect of carbon supply on allocation to allelochemicals and caterpillar consumption of peppermint. Oecologia **78**: 112–114.
- Little, E.C.S.** 1966. The invasion of man-made lakes by plants. Pages 75–86, in R.H. Lowe-McConnell (ed.) Man-made lakes. Academic Press, London.
- Lodge, D.M.** 1985. Macrophyte-gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshwater Biol. **15**: 695–708.
- . 1986. Selective grazing on periphyton: A determinant of freshwater gastropod microdistribution. Freshwater. Biol. **16**: 831–841.
- Loucks, O.L.** 1990. Land water interactions. Pages 243–258, in B.C. Patten, S.E. Jorgensen, H.J. Dumont, B. Gopal, P.P. Koryavov, J. Kvet, H. Löffler, Y.M. Sverizhev & J.G. Tundisi (eds.) Wetlands and shallow continental water bodies. Vol. 1. Natural and human relationships. SPB Academic Publishing, The Hague.
- Lovett-Doust, L.** 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus*). I. The dynamics of ramets in contrasting habitats. J. Ecol. **69**: 743–755.
- & **J. Lovett-Doust.** 1982. The battle strategies of plants. New Scientist **95**: 81–84.
- Maberly, S.C.** 1983. The interdependence of photon irradiance and free carbon dioxide on bicarbonate concentration on the photosynthetic compensation points of freshwater plants. New Phytol. **93**: 1–12.
- Madsen, J.D., J.W. Sutherland, J.A. Bloomfield, L.W. Eichler & C.W. Boylen.** 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. J. Aquatic Pl. Managem. **29**: 94–99.
- Maestrini, S.Y. & D.J. Bonin.** 1981. Allelopathic relationships between phytoplankton species: Algal ecology toxicity. Canad. Bull. Fish. Aquatic Sci. **209**: 323–338. Fisheries and Oceans, Govt of Canada, Ottawa.
- Malthus, T.R.** 1798. An essay on the principle of population. Penguin Books, Harmondsworth. (Reprinted ed. 1982).
- Martin, D.F.** 1983. Structural studies of a naturally occurring hydrilla inhibitor. Miscellaneous Paper A-83-2, US Army Engineer Waterways Experiment Station, Vicksburg, MS.



- Martin, B.B. & D.F. Martin.** 1988. Influence of substituted phenols on the growth of *Hydrilla*. J. Aquatic Pl. Managem. **26**: 74–75.
- May, F.E. & J.E. Ash.** 1990. An assessment of the allelopathic potential of *Eucalyptus*. Austral. J. Bot. **38**: 245–254.
- McClure, J.W.** 1970. Secondary constituents of aquatic angiosperms. Pages 233–265, in J.B. Harborne (ed.) Phytochemical Phylogeny. Academic Press. New York.
- & **R.E. Alston.** 1964. Nature **201**: 311. (cited from McClure 1970).
- McCracken, M.D., R.E. Middaugh & R.S. Middaugh.** 1980. A chemical characterization of an algal inhibitor obtained from *Chlamydomonas*. Hydrobiologia **70**: 271–276.
- McCreary, N.J.** 1985. Competition and coexistence in two vegetative perennials: *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett. Ph.D. thesis, University of Notre Dame, IN.
- . 1991. Competition as a mechanism of submersed macrophyte community structure. Aquatic Bot. **41**: 177–193.
- & **S.R. Carpenter.** 1983. Competition among submersed perennial plants: use of reciprocal replacement series in situ. Proceedings of the international symposium on aquatic macrophytes Nijmegen: 134–138.
- & ———. 1987. Density dependent growth interactions between *Eleocharis acicularis* (L.) R. & S. and *Juncus pelocarpus* forma *submersus* Fassett. Aquatic Bot. **27**: 229–241.
- , ——— & **J.E. Chaney.** 1983. Coexistence and interference in two submersed freshwater perennial plants. Oecologia **59**: 393–396.
- McIlraith, A.L., G.G.C. Robinson & J.M. Shay.** 1989. A field study of competition and interaction between *Lemna minor* and *Lemna trisulca*. Canad. J. Bot. **67**: 2904–2911.
- McLay, C.L.** 1974. The distribution of duckweed *Lemna perpusilla* in a small southern California lake: An experimental approach. Ecology **55**: 262–276.
- McMillan, C., O. Zapata & L. Escobar.** 1980. Sulphated phenolic compounds in seagrasses. Aquatic Bot. **8**: 267–278.
- McNaughton, S.J.** 1968. Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*. Ecology **49**: 367–369.
- Mehta, I. & R.K. Sharma.** 1975. Control of *Typha* by a competitive plant. Ann. Arid Zone **14**: 175–182.
- Meteiko, T. Ya.** 1981. Metabolites of higher aquatic plants and their role in hydrobiocoenoses: a review. (in Russian). Gidrobiologi Zhurnal **27**(4): 3–14.
- Misra, A., G.K. Patro & G.C. Tosh.** 1976. Studies on chemical control of *Chara*. Pages 265–268, in C.K. Varshney & J. Rzoska (eds.) Aquatic weeds in south east Asia. W. Junk, The Hague.
- Misra, R. D.** 1938. Edaphic factors in the distribution of aquatic plants in the English lakes. J. Ecol. **38**: 411–451.
- Moeller, R.E.** 1978. Seasonal changes in biomass, tissue chemistry and net production of the evergreen hydrophyte *Lobelia donmanna*. Canad. J. Bot. **56**: 1425–1433.
- Moen, R.A. & Y. Cohen.** 1989. Growth and competition between *Potamogeton pectinatus* L. and *Myriophyllum exalbescens* Fern. in experimental ecosystems. Aquatic Bot. **33**: 257–270.
- Moens, R.** 1981. Les habitats de *Lymnaea truncatula* hôte intermédiaire de *Fasciola hepatica*. Rev. Agric. **34**: 1563–1580.
- Mook, J.H. & J. van der Toorn.** 1982. The influence of environmental factors and management on stands of *Phragmites australis*. II. Effects on yield and its relationship with shoot density. J. Appl. Ecol. **19**: 501–517.
- Morton, B.A. & J.E. Keeley.** 1990. C4 acid fixation in photosynthesis of the submerged aquatic *Eleocharis acicularis* (L.) R. & S. Aquatic Bot. **36**: 379–388.
- Moss, B.** 1989. Water pollution and the management of ecosystems: A case study of science and scientist. Pages 401–422, in P.J. Grubb & J.B. Whittaker (eds.) Toward a more exact ecology. Blackwells, Oxford, U.K.
- Moyle, J.B.** 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Amer. Midl. Naturalist **34**: 402–420.

- Muller, C.H.** 1966. The role of chemical inhibition (allelopathy) in vegetational composition. *Bull. Torrey Bot. Club* **93**: 332–351.
- . 1969. Allelopathy as a factor in ecological process. *Vegetatio* **18**: 348–357.
- Munakata, K., S. Marumo, K. Ota & Y.L. Chen.** 1965. *Tetrahedron Lett.* 4167. (cited from McClure 1970).
- Myers, R.L.** 1984. Ecological compression of *Taxodium distichum* var. *nutans* by *Melaleuca quinquenervia* in southern Florida. Pages 358–364, in K.C. Ewel and H.T. Odum (eds) *Cypress swamps*. University of Florida Press, Gainesville, FL, USA.
- Nat. Acad. Sci.** 1976. Making aquatic weeds useful. Some perspectives for developing countries. National Academy of Sciences, Washington, D.C.
- Ndifon, G.T.** 1979. Studies on the feeding biology, anatomical variations and ecology of the vectors of Schistosomiasis and other freshwater snails in South Western Nigeria. Ph.D. Thesis, University of Ibadan, Ibadan, Nigeria.
- & **F.M.A. Ukoli.** 1989. Ecology of freshwater snails in South Western Nigeria. 1. Distribution and habitat preferences. *Hydrobiologia* **171**: 231–253.
- Niklas, K.J. & V. Kerchner.** 1984. Mechanical and photosynthetic constraints on the evolution of plant shape. *Paleobiology* **10**: 79–101.
- Numata, M.** 1982. Weed-ecological approaches to allelopathy. Pages 169–173, in W. Holzner & M. Numata (eds.). *Biology and ecology of weeds*. Dr. W. Junk Publ., The Hague.
- Nyberg, P.F.** 1986. Effects of allelopathic chemicals on photosynthetic rate of *Lemna minor*. MA Thesis, University of S. Dakota, Vermillion, SD, USA.
- Oborn, E.T., W.T. Moran, K.T. Greene & T.R. Bartley.** 1954. Weed control investigations on some important plants which impede flow of western irrigation waters. Joint Lab Report SI–2: 16–17. USDA Bureau of Reclamation Engineering Lab. & USDA ARS Field Crops Branch.
- O'Hara, J.** 1967. Invertebrates found in the water hyacinth mats. *Quart. J. Florida Acad. Sci.* **30**: 73–80.
- Okland, R.H.** 1990. Vegetation ecology: Theory, methods and applications with reference to Fennoscandia. *Sommerfeltia*, Suppl. **1**: 1–231.
- O'Neill Morin, J. & K.D. Kimball.** 1983. Relationship of macrophyte mediated changes in the water column to periphyton composition and abundance. *Freshwater Biol.* **13**: 403–414.
- Orth, R.J. & J. van Montfrans.** 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing. *Aquatic Bot.* **18**: 43–69.
- Ostrofsky, M.L. & E.R. Zettler.** 1986. Chemical defences in aquatic plants. *J. Ecol.* **74**: 279–284.
- Ozimek, T., E. Pieczynska & A. Hankiewicz.** 1991. Effects of filamentous algae on submerged macrophyte growth: a laboratory experiment. *Aquatic Bot.* **41**: 309–315.
- Parija, P.** 1934. Physiological investigations on waterhyacinth, *Eichhornia crassipes* in Orissa with notes on some other aquatic weeds. *Indian J. Agric. Sci.* **4**: 399–429.
- Patience, R.L., P.R. Sterry & J.D. Thomas.** 1983. Changes in chemical composition of a decomposing aquatic macrophyte, *Lemna paucicostata*. *J. Chem. Ecol.* **9**: 889–911.
- Patrick, Z., T. Toussoun & L. Koch.** 1964. Effect of crop residue decomposition products on plant roots. *Ann. Rev. Phytopath.* **2**: 267–292.
- Pawlowski, B. & K. Zarzycki.** 1972. Zespoły wodne i begienne. Pages 317–326, in W. Szafer & K. Zarzycki (eds.) *Szata roślinna polski*. 1. PWN, Warszawa, Poland.
- Pennak, R.W.** 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. *Trans. Amer. Microscop. Soc.* **85**: 329–349.
- . 1973. Some evidence for aquatic macrophytes as repellent for a limnetic species of *Daphnia*. *Int. Rev. Gesamten Hydrobiol.* **58**: 569–576.
- Philipose, M.T., V. Ramachandran, S.B. Singh & T. Ramaprabhu.** 1970. Some observations on the weeds of cultivable freshwaters in Orissa. *J. Inland Fish. Soc. India* **II**: 61–64.
- Phillips, G.L., D. Eminson & B. Moss.** 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Bot.* **4**: 103–126.
- Pianka, E.R.** 1981. Competition and niche theory. Pages 167–196, in R.M. May (ed.) *Theoretical ecology*. W.B. Saunders, Philadelphia.

- Pieczynska, E.** 1972. Ecology of the eulittoral zones of lakes. *Ekol. Pol.* **20**: 637–732.
- Pimentel, D. & P.C. White.** 1959. Biological environments and habits of *Australorbis glabratus*. *Ecology* **40**: 541–550.
- Pieterse, A.H. & K.J. Murphy** (eds) 1990. Aquatic weeds: The ecology and management of nuisance aquatic vegetation. Oxford University Press, Oxford, U.K.
- Pip, E.** 1984. Ecogeographical tolerance range variation in aquatic macrophytes. *Hydrobiologia* **108**: 37–48.
- . 1987. The ecology of *Potamogeton* species in central North America. *Hydrobiologia* **153**: 203–216.
- Ponnampuruma, F.N.** 1972. The chemistry of submerged soils. *Advan. Agron.* **24**: 29–96.
- Porwal, M.K. & S.L. Mundra.** 1992. Allelopathic effects of aqueous extracts of *Cyperus rotundus* and *Echinochloa colonum* on germination and growth of blackgram and paddy. Pages 87–88, in P. Tauro & S.S. Narwal (eds.) *Proc. first nat. symp. allelopathy in agroecosystems*. Indian Society of Allelopathy, Haryana Agric. University, Hissar, India.
- Pridham, J.B.** 1964. *Phytochemistry* **3**: 493. (cited from McClure, 1970).
- Proctor, V.W.** 1957. Some controlling factors in the distribution of *Haematococcus pluvialis*. *Ecology* **38**: 457–462.
- Putnam, A.R.** 1983. Allelopathic chemicals. Nature's herbicides in action. *Chem. Eng. News* **4**: 34–45.
- . 1988. Allelochemicals from plants as herbicides. *Weed Technol.* **2**: 510–518.
- & **C.S. Tang** (eds). 1986. *The Science of Allelopathy*. John Wiley, New York.
- Quackenbush, R.C., D. Bunn, & W. Lingren.** 1986. HPLC determination of phenolic acids in the water soluble extract of *Zostera marina* (L.) (Eelgrass). *Aquatic Bot.* **24**: 83–84.
- Rai, D.N. & J. DattaMunshi.** 1981. Ecological characteristics of chaurs of North Bihar. *Int. J. Ecol. Environ. Sci.* **7**: 89–98.
- , **P.K. Verma & J. DattaMunshi.** 1980. Interactions between a floating (*Trapa bispinosa*) and submerged vegetation community in a fishpond of Bhagalpur, India. *Pol. Arch. Hydrobiol.* **27**: 137–142.
- Ramaprabhu, T.** 1972. Observations on the autecology of *Ceratophyllum demersum* L. with notes on its control. *J. Asiat. Soc.* **14**: 149–162.
- Ramirez-Toro, G.I., G.R. Leather & F.A. Einhellig.** 1988. Effects of three phenolic compounds on *Lemna gibba* G3. *J. Chem. Ecol.* **14**: 845–853.
- Reavell, P.E.** 1980. A study of the diets of some British freshwater gastropods. *J. Concholl.* **30**: 253–271.
- Reddy, K.R.** 1988. Water hyacinth (*Eichhornia crassipes* (Mart.) Solms.) biomass cropping system. I. Production. Pages 103–140, in W.H. Smith & J.R. Frank (eds.) *Methane from biomass: A systems approach*. Elsevier, London.
- & **W.F. Debusk.** 1984. Growth characteristics of aquatic macrophytes cultured in nutrient enriched water: I. Water hyacinth, water lettuce and pennywort. *Econ. Bot.* **38(2)**: 229–239.
- & ———. 1985. Growth characteristics of aquatic macrophytes cultured in nutrient enriched water: II. *Azolla*, duckweed and *Salvinia*. *Econ. Bot.* **39(2)**: 200–205.
- , **D.L. Sutton & G.E. Bowes.** 1983. Biomass production of freshwater aquatic plants in Florida. *Proc. Soil. Crop Sci. Soc. Fl.* **42**: 28–40.
- Rejmankova, E.** 1975. Comparison of *Lemna gibba* and *Lemna minor* from the production ecological viewpoint. *Aquatic Bot.* **1**: 423–428.
- Reznik, H. & R. Neuhausel.** 1959. *Z. Bot.* **47**: 41. (cited from McClure 1970).
- Rhoades, D.F. & R.G. Cates.** 1976. Toward a general theory of plant anti-herbivore chemistry. *Recent Advances Phytochem.* **10**: 168–213.
- Rice, E.L.** 1967. Chemical warfare between plants. *Bios* **38**: 67–74.
- . 1974. *Allelopathy*. First Edition. Academic Press, N.Y.
- . 1979. *Allelopathy: an update*. *Bot. Rev.* **45**: 15–109.
- . 1984. *Allelopathy*. 2nd Edition. Academic Press, N.Y.
- Rogers, K.H. & C.M. Breen.** 1983. An investigation of macrophyte, epiphyte and grazer interactions. Pages 217–226, in R.G. Wetzel (ed.) *Periphyton of freshwater ecosystems*. Develop. Hydrobiol. **17**. W. Junk, The Hague.

- Sanchez Tames, R., M.D.V. Gesto & E. Vieitez.** 1973. Growth substances isolated from tubers of *Cyperus esculentus* var. *aureus*. *Physiol. Pl.* **28**: 195-200.
- Sankaran, T. & V.P. Rao.** 1972. An annotated list of insects attacking some terrestrial and aquatic weeds in India with records of some parasites of the phytophagous insects. *Techn. Bull. Commonw. Inst. Biol. Control* **15**: 131-157.
- Saxena, Manjula K.** 1991. Effect of terrestrial litter inputs on the growth of aquatic plants. International conference on land-water interactions, Abstracts: 147. National Institute of Ecology, New Delhi.
- . 1992. Allelopathic potential of terrestrial plants against the growth of aquatic weeds. Pages 147-148, in P. Tauro & S.S. Narwal (eds) *Proc. first nat. symp. allelopathy in agroecosystems*. Indian Society of Allelopathy, Haryana Agric. University, Hissar, India.
- Schloesser, D.W., T.A. Edsall & B.A. Manny.** 1985. Growth of submersed macrophyte communities in the St. Clair-Detroit river system between Lake Huron and Lake Erie. *Canad. J. Bot.* **63**: 1061-1065.
- Schreiter, T.** 1928. Untersuchungen über den Einfluss einer Helodeawucherung auf die Netzplankton des Hirschberger Grossteiches in Bohmen in den Jahren 1921 bis 1925 incl. *Sb. vyzk. Ust. zemed.* RCS 61.
- Scholes, K.** 1987. Effects of six classes of allelochemicals on growth, photosynthesis, and chlorophyll content in *Lemna minor*. MA thesis, University of S. Dakota, Vermillion, SD, USA.
- Schröder, R.** 1987. Das Schilfsterben am Bodensee-Untersee: Beobachtungen, Untersuchungen und Gegenmassnahmen. *Arch. Hydrobiol. Suppl.* **76**: 53-99.
- Sculthorpe, C.D.** 1967. The biology of aquatic vascular plants. Edward Arnold, London.
- Segal, S.** 1968. On structure, zonation and succession in vegetation of higher aquatics. Manuscript to Expert Meeting on Ecology and Control of Aquatic Vegetation. UNESCO, Paris.
- Seidel, K.** 1965. Phenol-Abbau in Wasser durch *Scirpus lacustris* L. während einer versuchsdauer von 31 Monaten. *Naturwissenschaften* **52(13)**: 398-399.
- . 1969. Zur bakteriziden Wirkung höherer Pflanzen. *Naturwissenschaften* **56(12)**: 642-643.
- . 1971a. Wirkung höherer Pflanzen auf pathogene Keime in Gewässern. *Naturwissenschaften* **58(4)**: 150-151.
- . 1971b. Macrophytes as functional elements in the environment of man. *Hidrobiologia, Bucuresti* **12**: 121-130.
- . 1972. Exudat-Effekt der Rhizothamnien von *Alnus glutinosa* Gaertner. *Naturwissenschaften* **59(8)**: 366-367.
- . 1973. Zur Biologie und Gewässer-Reinigungsvermögen von *Iris pseudoacorus* L. *Naturwissenschaften* **60(3)**: 158.
- . 1974. *Schoenoplectus lacustris* (L.) Palla zur Reinigung von Gewässern. *Naturwissenschaften* **61(2)**: 81.
- & **R. Kickuth.** 1970. Wasser und Boden 1970: 38-40. (cited from Seidel, 1971b).
- Sharma, K.P.** 1985. Allelopathic influence of algae on the growth of *Eichhornia crassipes* (Mart.) Solms. *Aquatic Bot.* **22**: 71-78.
- & **B. Gopal.** 1978. Seed germination and occurrence of seedlings of *Typha* species in nature. *Aquatic Bot.* **4**: 353-358.
- & ———. 1979a. Effect of light intensity on growth and establishment of seedlings of *Typha angustata*. *Pol. Arch. Hydrobiol.* **26**: 495-500.
- & ———. 1979b. Effect of water regimes on the growth and establishment of *Typha angustata* seedlings. *Int. J. Ecol. Environm. Sci.* **5**: 69-74.
- & ———. 1980. A note on the identity of *Typhaelephantina* Roxb. *Aquatic Bot.* **9**: 381-387.
- , **S.P.S. Khushwaha & B. Gopal.** 1990. Autotoxic effect on *Phragmites karka* (Retz) Trin. ex Steud. plant on its seed germination. *Geobios* **17**: 287-288.
- & **V.N. Pradhan.** 1983. Study on growth and biomass of underground organs of *Typha angustata* Bory et Chaub. *Hidrobiologia* **98**: 147-151.
- Sheldon, S.P.** 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* **68**: 1920-1931.

- Silverstein, R.M. & J.B. Simeone** (eds.). 1983. Special issue: American Chemical Society Symposium on Allelopathy. *J. Chem. Ecol.* **9**: 1–935.
- Simberloff, D.** 1983. Competition theory, hypothesis testing and other community ecological buzzwords. *Amer. Naturalist* **122**: 626–635.
- Simpson, P.S. & J.W. Eaton.** 1986. Comparative studies of the photosynthesis of the submerged macrophyte *Elodea canadensis* and the filamentous algae *Cladophora glomerata* and *Spirogyra* sp. *Aquatic Bot.* **24**: 1–12.
- Singh, D. & R.K. Kohli.** 1992. Reasons of poor under floor vegetation of *Eucalyptus*. Pages 114–117, in P. Tauro & S.S. Narwal (eds.) *Proc. first nat. symp. allelopathy in agroecosystems*. Indian Society of Allelopathy, Haryana Agric. University, Hissar, India.
- Singh, Mohan.** 1992. Studies on growth, competition and allelopathic interactions among aquatic macrophytes. Ph.D. thesis, University of Rajasthan, Jaipur, India.
- Singh, S.P.** 1968. Presence of growth inhibitor in the tubers of nutgrass (*Cyperus rotundus* L.). *Proc. Indian Acad. Sci.* **67**: 18–23.
- Singhvi, N.R. & K.D. Sharma.** 1984. Allelopathic effects of *Ludwigia adscendens* Linn. and *Ipomoea aquatica* Forsk. on seedling growth of pearl millet (*Pennisetum typhoides* Rich.). *Trans. Isdt. and Ucds.* **9**(2): 95–100.
- Sinhbabu, A. & D.P. Kushari.** 1984. Effect of leaf leachates of *Polyalthia longifolia* on the growth and nitrogen fixation of *Azolla pinnata*. *Hydrobiol. Bull.* **18**(2): 103–108.
- Sircar, P.K. S. Banerjee & S.M. Sircar.** 1973. Gibberellin like activity in the shoot extract of water hyacinth (*Eichhornia crassipes*). *Indian J. Agric. Sci.* **43**: 1–8.
- Sircar, S.M. & R. Chakraverty.** 1961. The effect of growth regulating substances of the root extract of water hyacinth (*Eichhornia speciosa* Kunth.) on jute (*Corchorus capsularis* Linn.). *Curr. Sci.* **11**: 428–430.
- & ———. The effect of gibberellic acid and growth regulating substances of the root extract of water hyacinth (*Eichhornia crassipes*) on rice and gram. *Indian J. Pl. Physiol.* **5**: 257–263.
- & **M. Kundu.** 1959. Effect of root extract of water hyacinth (*Eichhornia speciosa* Kunth) on the growth and flowering of rice. *Sci. & Cult.* **24**: 332–333.
- & ———. 1960. Growth regulating properties of root extract of *Eichhornia speciosa* Kunth. *Physiol. Pl.* **13**: 56–63.
- Smart, R.M. & J.W. Barko.** 1989. Competitive interactions of submersed aquatic macrophytes in relation to water chemistry and other environmental conditions. Pages 159–164, in *Proceedings of the 23rd Annual meeting on the aquatic plant control research program*. MP-A-89-1. USAE-WES, Vicksburg, MS.
- Smith, C.S.** 1978. Phosphorus uptake by roots and shoots of *Myriophyllum spicatum* L. Ph.D. thesis, Univ. of Wisconsin, Madison.
- Smock, L.A. & D.L. Stoneburner.** 1980. The response of macroinvertebrates to aquatic macrophyte decomposition. *Oikos* **33**: 397–403.
- Sondergaard, M.** 1983. Heterotrophic utilization and decomposition of extracellular carbon released by the aquatic angiosperm *Littorella uniflora* (L.) Aschers. *Aquatic Bot.* **16**: 59–75.
- . 1988. Photosynthesis of aquatic plants under natural conditions. Pages 63–111, in J.J. Symoens (ed.) *Vegetation of inland waters. Handbook of vegetation science 15/1*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Spence, D.H.N.** 1982. The zonation of plants in freshwater lakes. *Advan. Ecol. Res.* **12**: 37–125.
- Spencer, N.R. & M. Lekic.** 1974. Prospects for biological control of Eurasian Watermilfoil. *Weed Sci.* **22**(4): 401–404.
- Spencer, D.F.** 1988. Competition between two pondweeds: Influence of *P. pectinatus* tuber size. *Internat. Symposium on physiological ecology of aquatic plants, aarhus, Denmark*. Abstracts.
- & **W. van Vierssen.** 1988. Competition and the distribution of two submersed macrophytes in an irrigation canal. *Bull. Ecol. Soc. Amer.* **69**(2): 304.
- Spoehr, H.A., J.H.C. Smith, H.H. Strain, H.W. Milner & G.J. Hardin.** 1949. *Carnegie Inst. Washington Publ.* 586. (cited from Rice 1984).

- Srivastava, P.R. & L.K. Das.** 1974. Effect of certain aqueous plant extracts on the germination of *Cyperus rotundus* L. *Sci. & Cult.* **40**(7): 318–319.
- Stangenberg, M.** 1968. Bacteriostatic effects of some algae and *Lemna minor* extracts. *Hydrobiologia* **32**: 88–96.
- Steeman-Nielsen, E.** 1947. Photosynthesis of aquatic plants with special reference to the carbon sources. *Dansk Botanisk Arkiv*. **12**: 1–71.
- . 1973. *Hydrobiologi*. Polyteknisk Forlag, Lyngby.
- Sterry, P.R., J.D. Thomas & R.L. Patience.** 1983. Behavioural responses of *Biomphalaria glabrata* (Say) to chemical factors from aquatic macrophytes including decaying *Lemna paucicostata* and *Ceratophyllum demersum*. *Freshwater Biol.* **13**: 465–476.
- , ——— & ———. 1985. Changes in the concentration of short-chain carboxylic acids and gases during decomposition of the aquatic macrophytes *Lemna paucicostata* and *Ceratophyllum demersum*. *Freshwater Biol.* **15**: 139–153.
- Stevens, K.L. & G.B. Merrill.** 1980. Growth inhibitors from spikerush. *J. Agric. Food Chem.* **28**: 644–646.
- Steward, K.K.** 1988. Competitive interaction between monoecious *Hydrilla* and *Vallisneria* on soils of varying fertility. Final Report USDI-NPS/USDA-ARS, Fort Lauderdale, FL.
- Stom, D.I. & R. Roth.** 1981. Some effects of polyphenols on aquatic plants: 1. Toxicity of phenols in aquatic plants. *Bull. Environm. Contam. Toxicol.* **27**: 332–337.
- Su, K.L., Y. Abul-Hajj & E.J. Staba.** 1973a. Antimicrobial effects of aquatic plants from Minnesota. *Lloydia* **36**: 80–87.
- & **E.J. Staba.** 1973. Toxicity, anti-neoplastic and coagulation effects of aquatic plants from Minnesota. *Lloydia* **36**: 99–102.
- , ——— & **Y. Abul-Hajj.** 1973b. Preliminary chemical studies of aquatic plants from Minnesota. *Lloydia* **35**: 72–79.
- Sutton, D.L.** 1986a. Growth of hydrilla (*Hydrilla verticillata*) in established stands of spikerush and slender arrowhead. *J. Aquatic Pl. Managem.* **24**: 16–20.
- . 1986b. Influence of allelopathic chemicals on sprouting of hydrilla tubers. *J. Aquatic Pl. Managem.* **24**: 88–90.
- . 1990. Growth of *Sagittaria subulata* and interaction with hydrilla. *J. Aquatic Pl. Managem.* **28**: 20–22.
- , **R.C. Littel & K.A. Langeland.** 1980. Intraspecific competition of *Hydrilla verticillata*. *Weed Sci.* **28**: 425–428.
- & **K.M. Portier.** 1989. Influence of allelochemicals and aqueous plant extracts on growth of duckweed. *J. Aquatic Pl. Managem.* **27**: 90–95.
- & ———. 1991. Influence of spikerush plants on growth and nutrient content of hydrilla. *J. Aquatic Pl. Managem.* **29**: 6–11.
- Svedang, M.U.** 1990. The growth dynamics of *Juncus bulbosus* - a strategy to avoid competition. *Aquatic Bot.* **37**: 123–138.
- Swindale, D.N. & J.T. Curtis.** 1957. Phytosociology of the larger submerged plants in Winsconsin lakes. *Ecology* **38**: 397–407.
- Szczepanska, W.** 1971. Allelopathy among the aquatic plants. *Pol. Arch. Hydrobiol.* **18**: 17–30.
- . 1977a. Interactions of *Phragmites communis* Trin. and *Carex hudsonii* Benett. *Ekol. Pol.* **24**: 431–436.
- . 1977b. The effect of remains of helophytes on the growth of *Phragmites communis* Trin. and *Typha latifolia* L. *Ekol. Pol.* **25**: 437–445.
- . 1987. Allelopathy in helophytes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **27**: 173–179.
- & **A.J. Szczepanski.** 1982. Interactions between *Phragmites australis* (Cav.) Trin. ex Steud. and *Typha latifolia* L. *Ekol. Pol.* **30**(1–2): 165–186.
- Szczepanski, A.J.** 1971. Allelopathy and other factors controlling the macrophytes production. *Hydrobiologia* **12**: 193–197.
- . 1977. Allelopathy as a means of biological control of water weeds. *Aquatic Bot.* **3**: 193–197.



- Tag el Seed, M.** 1978. Effect of pH on the nature of competition between *E. crassipes* and *Pistia stratiotes*. *J. Aquatic Pl. Managem.* **16**: 53–57.
- Taheruzzaman, Q. & D.P. Kushari.** 1991. Influence of leaf leachate enriched water of neem (*Azadirachia indica* A.Jun.) and shirish (*Albizia lebbek* Benth.) on the growth of *Eichhornia crassipes* (Mart.) Solms. *Aquatic Bot.* **40**: 1–9.
- Thomas, J.D.** 1987. An evaluation of the interactions between freshwater pulmonate snail hosts of human schistosomes and macrophytes. *Phil. Trans. R. Soc. London B* **315**: 75–125.
- . 1990. Mutualistic interactions in freshwater modular systems with molluscan components. *Adv. Ecol. Res.* **20**: 125–178.
- & **A.I. Tait.** 1984. Control of the snail hosts of schistosomiasis by environmental manipulation: A field and laboratory appraisal in the Ibadan area of Nigeria. *Phil. Trans. R. Soc. London B* **305**: 201–253.
- Thompson, K.** 1987. The resource ratio hypothesis and the meaning of competition. *Funct. Ecol.* **1**: 297–303.
- Tilman, D.** 1987. On the meaning of competition and the mechanism of competitive superiority. *Funct. Ecol.* **1**: 304–315.
- . 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.
- Titus, J.E. & M.S. Adams.** 1979. Coexistence and the comparative light relations of the submersed macrophytes, *Myriophyllum spicatum* (L.) and *Vallisneria americana* Michx. *Oecologia* **40**: 273–286.
- & **M.D. Stephens.** 1983. Neighbour influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. *Oecologia* **56**: 23–29.
- Tripathi, R.S. & P.P. Srivastava.** 1970. Effect of aqueous plant extracts on the seed germination of *Lycopersicon esculentum* Mill. *Sci. & Cult.* **36**(1): 59–60.
- Tucker, C.S.** 1983. Culture density and productivity of *Pistia stratiotes*. *J. Aquatic Pl. Managem.* **21**: 40–41.
- Tüxen, R. & E. Preising.** 1942. Grundbegriffe und Methoden zum Studium der Wasser- und Sumpfpflanzengesellschaften. *Dtsch. Wasserwirtschaft* **37**: 10–17, 57–69.
- Underwood, G.J.C.** 1989. Interactions between freshwater pulmonate snails, macrophytes and epiphytes. D. Phil. thesis, Univ. of Sussex, Sussex, U.K.
- Van Aller, R.T., L.R. Clark, G.F. Pessoney & V.A. Rogers.** 1983. A prostaglandin like fatty acid from a species in the cyperaceae. *Lipids* **18**(9): 617–621.
- , **G.F. Pessoney, V.A. Rogers, E.J. Watkins & H.G. Leggett.** 1985. Oxygenated fatty acids: A class of allelochemicals from aquatic plants. Pages 387–400, in A.C. Thompson (ed.) *The chemistry of allelopathy*. ACS Symposium series 268. American Chemical Society, Washington, D.C. USA.
- Van, T.K., W.T. Haller & G. Bowes.** 1976. Comparison of the photosynthetic characteristics of three submerged aquatic plants. *Pl. Physiol.* **58**: 761–768.
- Van der Valk, A.G.** 1981. Succession in wetlands: a Gleasonian approach. *Ecology* **62**: 688–696.
- . 1987. Vegetation dynamics of freshwater wetlands: A selective review of the literature. *Arch. Hydrobiol. Beiheft. Ergebn. limnol.* **27**: 27–40.
- & **C.B. Davis.** 1976. Changes in the composition, structure and production of plant communities along a perturbed wetland coenocline. *Vegetatio* **32**: 87–96.
- & ———. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**: 322–335.
- van Montfrans, J., R.J. Orth & S.A. Vay.** 1982. Primary studies of grazing by *Bittium varium* on eelgrass periphyton. *Aquatic Bot.* **14**: 75–89.
- , **R.L. Wetzel & R.J. Orth.** 1984. Epiphyte-grazer relationships in seagrass meadows: Consequences of seagrass growth and production. *Estuaries* **7**: 289–309.
- Van Schayck, I.C.P.** 1985. Laboratory studies on the relation between aquatic vegetation and the presence of two *Bilharzia*-bearing snail species. *J. Aquatic Pl. Managem.* **23**: 87–91.
- Wajih, S.A. & A.C. Sinha.** 1980. Growth regulating substances in the algal extracts of *Chara zeylanica* Kl. ex Willd. *Indian J. Ecol.* **7**: 158–160.

- Wallace, J.W., T.J. Mabry & R.E. Alston.** 1969. Phytochemistry **8**: 93.
- Weidenhamer, J.D., D.C. Hartnett & J.T. Romeo.** 1989. Density- dependent phytotoxicity: Distinguishing resource competition and allelopathic interference in plants. *J. Appl. Ecol.* **26**: 613–624.
- Werner, D. & H. Pawlitz.** 1978. *Bull. Environ. Contam. Toxicol.* **20**: 303. (cited from Stom & Roth, 1981).
- Westlake, D.F.** (coordinator) 1980. Primary production. Pages 141–246, *in* E.D. LeCren & R.H. Lowe-McConnell (eds) *The functioning of freshwater ecosystems*. Cambridge University Press, London, U.K..
- . 1981. Temporal changes in aquatic macrophytes and their environment. *Dynamique de populations et qualite de l' Eau.*: 110–138.
- Wetzel, R.G.** 1969. Factors influencing photosynthesis and excretion of dissolved organic matter by aquatic macrophytes in hard water lakes. *Verh. Int. Verein. Limnol.* **17**: 72–85.
- . 1983a. Attached algal substrate interactions. Fact or myth and when and how? Pages 207–215, *in* R.G. Wetzel (ed.) *Periphyton of freshwater ecosystems*. Develop. Hydrobiol. **17**. W. Junk, The Hague.
- . 1983b. *Limnology*. 2ed. Saunders College Publishing, Philadelphia, PA.
- . 1988. Water as an environment for plant life. Pages 113–154, *in* J.J. Symoens (ed.) *Vegetation of inland waters*. Handbook of vegetation science 15/1. Kluwer Academic Publishers, Dordrecht.
- . 1990. Land-water interface: Metabolic and limnologic regulators. *Verh. Int. Ver. Limnol.* **24**: 6–24.
- & **R.A. Hough.** 1973. Productivity and role of aquatic macrophytes in lakes: An assessment. *Pol. Arch. Hydrobiol.* **20**: 9–19.
- Whigham, D.F., R.L. Simpson & M.A. Leck.** 1979. The distribution of seeds, seedlings and established plants of Arrow arum (*Peltandra virginica* (L.) Kunth.) in a freshwater tidal wetland. *Bull. Torrey Bot. Club* **106**(3): 193–199.
- Whittaker, R.H. & P.P. Feeney.** 1971. Allelochemicals: Chemical interactions between species. *Science* **171**: 757–770.
- Willaman, J.J. & B.G. Schubert.** 1961. Alkaloid bearing plants and their contained alkaloids. *Tech. Bull.* 1234. U.S. Dept Agric., Washington, D.C.
- Williamson, G.B.** 1990. Allelopathy, Koch's postulates and the neck riddle. Pages 143–162, *in* J.B. Grace & D. Tilman (eds.) *Perspectives on plant competition*. Academic Press, San Diego, CA, USA.
- Wilson, S.D. & P.A. Keddy.** 1985a. The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: An experimental study. *Aquatic Bot.* **21**: 277–284.
- & ———. 1985b. Plant zonation on a shoreline gradient: Physiological response curves of component species. *J. Ecol.* **73**: 851– 860.
- & ———. 1986a. Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. *Amer. Naturalist* **127**: 862–869.
- & ———. 1986b. Species competitive ability and position along a natural stress/disturbance gradient: Results. *Ecology* **67**: 1236– 1242.
- & ———. 1991. Competition, survivorship and growth in macrophyte communities. *Freshwater Biol.* **25**: 331–337.
- Wium-Anderson, S.** 1987. Allelopathy among aquatic plants. *Arch. Hydrobiol. Beih., Ergebn. Limnol.* **27**: 167–172.
- , **U. Anthoni, C. Christopherson & G. Houen.** 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). *Oikos* **39**: 187– 190.
- , ——— & **G. Houen.** 1983. Elemental sulphur, a possible allelopathic compound from *Ceratophyllum demersum*. *Phytochemistry* **22**(11): 2613.
- & **J. Borum.** 1980. Biomass and production of eelgrass (*Zostera marina* L.) in the Oresund, Denmark. *Ophelia* **19**(1): 49–55.
- & ———. 1984. Biomass variation and autotrophic production of an epiphyte-macrophyte community in a coastal Danish area. 1. Eelgrass (*Zostera marina* L.) biomass and net production. *Ophelia* **23**(1): 33–46.

- Wolek, J.** 1974. A preliminary investigation on interactions (competition, allelopathy) between some species of *Lemna*, *Spirodela* and *Wolffia*. Ber. Geobot. Inst. Eidg. Techn. Hochschule, Stift. Rübel, **42**: 140–162.
- . 1979. Competition and allelopathy between *Spirodela polyrrhiza* and *Wolffia arrhiza*. Fragn. Flor. Geobot. (Cracow) **25(2)**: 281–350.
- . 1984. Intraspecific variation and the competitive abilities of *Spirodela polyrrhiza* (L.) Schleiden. Ekol. Pol. **32**: 637–649.
- Wolfe, J.M. & E.L. Rice.** 1979. Allelopathic interactions among algae. J. Chem. Ecol. **5**: 533–542.
- Wooten, J.W. & S.D. Elakovich.** 1991. Comparisons of potential allelopathy of seven freshwater species of spikerushes (*Eleocharis*). J. Aquatic Pl. Managem. **29**: 12–15.
- Wrobel, J.T.** 1967. *Nuphar* alkaloids. Pages 441–465, in R.H.F. Manske (ed.) The alkaloids: chemistry and physiology. Academic Press, N.Y.
- Yamasaki, S.** 1990. Population dynamics in overlapping zones of *Phragmites australis* and *Miscanthus saccharifolius*. Aquatic Bot. **36**: 367–377.
- Yan, N.D., G.E. Miller, I. Wile & G.G. Hitchin.** 1985. Richness of aquatic macrophyte floras of softwater lakes of differing pH and trace metal content in Ontario, Canada. Aquatic Bot. **23**: 27–40.
- Yeo, R.R.** 1972. Control of rooted submerged aquatic weeds with competitive plants. Weed Science Society of America, Meeting Abstracts, St Louis, MO.
- . 1976. Naturally occurring antagonistic relationships among aquatic plants that may be useful in their management. Pages 290–293, in Proceedings IV Intern. Symp. Biol. Control Weeds, Gainesville, FL.
- . 1980. Spikerush may help control water weeds. Calif. Agric. **34**: 13–14.
- . 1980. Life history and ecology of dwarf spikerush (*Eleocharis coloradoensis*). Weed Sci. **28**: 263–272.
- & **T.W. Fisher.** 1970. Progress and potential for biological weed control with fish, pathogens, competitive plants and snails. Pages 450–463 in Technical papers of FAO international conference on weed control, June 22–July 1. Weed Science Society of America, Davis, CA.
- & **J.R. Thurston.** 1984. The effect of dwarf spikerush (*Eleocharis coloradoensis*) on several submersed aquatic weeds. J. Aquatic Pl. Managem. **22**: 52–56.
- Yoda, K., T. Kira, H. Ogawa & K. Hozumi.** 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). J. Biol., Osaka City Univ. **14**: 107–129.
- Zapata, O. & C. McMillan.** 1979. Phenolic acids in seagrasses. Aquatic Bot. **7**: 307–317.
- Zutshi, D.P. & K.K. Vass.** 1976. Ecology of macrophytic vegetation of Kashmir lakes. Pages 141–146, in C.K. Varshney & J. Rzoska (eds.) Aquatic weeds in south east Asia. W. Junk, The Hague.