

Journal of Range Management

Publication
of the
Society for
Range Management



The Trail Boss

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Published bimonthly—January, March, May, July, September, November

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EDITORIAL CORRESPONDENCE, concerning manuscripts or other editorial matters, should be addressed to the Editor, Gary Frasier, 1300 Wheatridge Ct., Loveland, Colorado 80537. Page proofs should be returned to the Production Editor, 1839 York Street, Denver, Colorado 80206.

INSTRUCTIONS FOR AUTHORS appear on the inside back cover of most issues. A Style Manual is also available from the Society for Range Management at the above address @\$2.00 for single copies; \$1.25 each for 2 or more.

THE JOURNAL OF RANGE MANAGEMENT (ISSN 0022-409X) is published six times yearly for \$56.00 per year by the Society for Range Management, 1839 York Street, Denver, Colorado 80206. SECOND CLASS POSTAGE paid at Denver, Colorado.

POSTMASTER: Return entire journal with address change—RETURN POSTAGE GUARANTEED—to Society for Range Management, 1839 York Street, Denver, Colorado 80206.

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- to properly take care of the basic rangeland resources of soil, plants and water;
- to develop an understanding of range ecosystems and of the principles applicable to the management of range resources;
- to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;
- to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;
- to create a public appreciation of the economic and social benefits to be obtained from the range environment;
- to promote professional development of its members.

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Invited Synthesis Paper

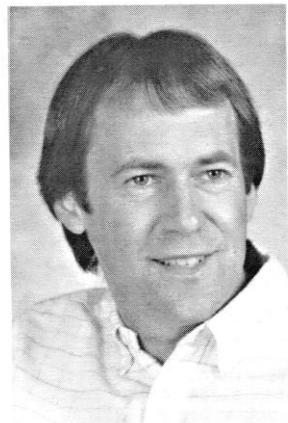
The Editorial Board of the *Journal of Range Management* invited Michael B. Coughenour to prepare this synthesis paper.

MICHAEL B. COUGHENOUR has offered important insights into processes regulating responses of plants to grazing by large herbivores. He has often applied a clear understanding of the physiology of individuals to explain mechanisms operating at higher levels of ecological organization.

Michael received Bachelor and Master of Science degrees in biology from the University of Illinois and his Doctor of Philosophy in systems ecology from Colorado State University. His doctoral work focused on impacts of SO₂ emissions on the sulphur cycle in grassland ecosystems. During 1978–1983, he was a post-doctoral fellow in the laboratory of Sam McNaughton at Syracuse University, where he developed simulation models of primary production of east African grasses. Since then, Michael has been a research scientist at the Natural Resource Ecology Laboratory at Colorado State University, and has worked on a variety of ecosystem studies in east Africa and in Yellowstone National Park.

Michael has published many influential papers. The hallmark of his writing is an unusual ability to assemble knowledge from diverse sources—from experiment, from scholarship, and from simulation. He brings this information to bear in revealing ways on important questions in contemporary ecology.

Michael lives with his wife, Cindy, and their daughter, Jordan, in the foothills west of Fort Collins, Colorado.



Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems

MICHAEL B. COUGHENOUR

Abstract

The spatial component of herbivory remains enigmatic although it is a central aspect of domestic and native ungulate ecosystems. The effects of ungulate movement on plants have not been clearly established in either range or wildlife management. While livestock movement systems have been implemented to cope with increases in livestock density, restrictions on movement, and overgrazing, a large number of studies have disputed the effectiveness of different livestock movement patterns. Traditional pastoralism, particularly nomadism, has been perceived as irrational and even destructive, but many studies have documented features of traditional pastoral land use that would promote sustainability. Disruptions of wild ungulate movements have been blamed for wildlife overgrazing and population declines, but actual patterns and mechanisms of disrupted movement and population responses have been poorly documented.

Models that integrate plant growth, ungulate movement, and foraging are suggested as a way to improve analyses of spatial plant-herbivore systems. Models must give due attention to non-forage constraints on herbivore distribution, such as topography. Models should assess the significance of movement as a means of coping with local climatic variation (patchy rainfall). Models that distribute an aggregate population over a landscape in relation to the distribution of habitat features deemphasize aspects of ungulate movements and population responses that inevitably cause nonideal distributions, particularly in natural ecosystems. Individual based models describe movement and foraging processes more accurately, but these models are difficult to apply over large areas. Both top-down and bottom-up approaches to spatial herbivory are needed. To model plant responses to movement, it is important to account for small scale phenomena such as tiller

defoliation patterns, patch grazing, and grazing lawns as well as large scale patterns such as rotation and migration. Herbivory patterns at these different scales are interrelated.

Managers of wildlife and domestic livestock populations confront similar problems as they attempt to interpret ungulate spatial distribution patterns and their effects on plants. Overgrazing and subsequent ecosystem degradation on rangelands or pastoral grazing areas are often attributed to inappropriate management of livestock spatial distributions. Overabundances of ungulates in wildlife preserves, and consequent overgrazing, are often attributed to human interference with natural ungulate migrations or dispersal patterns. These management problems are analogous in that ungulate spatial utilization patterns determine how grazing impacts are distributed in space and in time. Ecosystem sustainability is affected by interactions among animal movement and abundance, plant growth, plant response to grazing, and the physical structure of the landscape.

The consequences of herbivory for ecosystems depend, of course, upon herbivore abundance. However, herbivore abundance is expressed in terms of numbers of animals per unit of land, per unit of plant production, or per unit of land per unit time. These measures have been distinguished as stocking density, grazing pressure, and stocking rate, respectively (Heitschmidt and Taylor 1991). Until recently, research and management of ungulate herbivores have treated the denominators of these expressions as homogeneous. The aim of this paper is to explore heterogeneities in these denominators that are normally averaged out.

Although livestock spatial distributions have been manipulated in relation to forage availability for thousands of years, a meager amount of scientific attention has been devoted to the spatial components of herbivory. Spatial management is often based on tradition, trial and error, subjective judgements, or poorly defined

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This research was supported by NSF grant BSR-900 73003. The manuscript was constructively reviewed by N. Thomas Hobbs, Rodney Heitschmidt, and Douglas Frank.

conceptual models. Although spatio-temporal distribution patterns apparently affect plants and livestock productivity and explain wildlife overabundances and overgrazing, a stronger scientific foundation is needed to support these perceptions.

The difficulty of uniting a wide range of disciplines has undoubtedly slowed progress in the science of spatial plant-herbivore interactions. Synthetic studies are needed which link landscape ecology, geography, anthropology, plant ecology, and ungulate biology and behavior. Plant responses to herbivory must be integrated with ungulate spatial distributions. Effects of ungulate behavioral processes on movement must be considered, as well as effects of culture and human behavior in pastoral systems. Population dynamics come into play in native ungulate ecosystems.

Spatial heterogeneity has not been included in the mathematical models of plant-herbivore systems that have had the greatest impacts on wildlife management (e.g., Caughey 1976b, Walker et al. 1981, Crawley 1983). The quest for mathematical simplicity and analytical tractability in models has, unfortunately, also precluded considerations of the spatial components of plant-herbivore interactions. However, computer models have recently become sophisticated enough to simulate realistic spatial interactions. Large amounts of information are involved in spatial analyses but computerized techniques for spatial data storage and analysis have advanced greatly.

The principal aim of this paper is to reexamine the spatial elements of herbivory in both domestic and native ungulate ecosystems, synthesizing knowledge from a wide range of disciplines. I assess what is known about effects of ungulate movements and distributions on their interactions with plants and propose elements of a framework for analyses of spatially extensive plant-ungulate ecosystems. The first element of this framework is quantification of the effects of nonforage factors on ungulate distributions. Models of ungulate distributions and movements and plant responses to resultant grazing regimes are additional components. The final element draws from theory of the consequences of spatial heterogeneity for ecosystem stability.

Spatial Herbivory Patterns in Ranching Ecosystems

When livestock numbers increased dramatically in the western U.S. in the late nineteenth century, there was little management of livestock numbers or distributions to prevent overgrazing. Early American cattle and sheep herders exploited space in a nomadic manner. But the open ranges were greatly restricted from 1912 to 1925 with the influx of homesteaders (Cole et al. 1927). Early cattlemen looked upon settlers with disfavor because their fences prevented open range herds from "drifting with the storms" (Vass 1926). When fences were encountered, stock simply "walked back and forth along them until they became exhausted".

Large numbers of livestock were imported from the midwest by rail and from the south along cattle trails. The carrying capacity of the open range was quickly exceeded. The loss of flexibility in nomadic movement, increasing competition, and associated problems of overgrazing were reasons for early implementations of grazing systems. Seasonal adjustments in livestock distribution were imposed to compensate for lack of freedom of movement (Bell 1978).

Jared Smith, who was the first to advocate seasonal or deferred grazing (Smith 1895), saw that many grasslands had evolved under intermittent grazing by native migratory ungulates. He alluded to the state of affairs of only 30 years prior, when millions of bison roamed and moved naturally, permitting alternating periods of pasturing and rest (Smith 1899). Severe livestock overgrazing from 1885 to 1899 prompted him to suggest "partial resting", a system of alternating grazing among smaller subdivided pastures.

Many early grazing schemes were developed in mountainous

terrain (e.g., Cotton 1907). Jardine (1912) suggested that mountain ranges should not be close grazed in the first half of the year every year, so he designed a deferred rotation system. Some of Sampson's first tests of deferred grazing were in the mountains of Oregon (Sampson 1913), and in the high summer range in Utah (Sampson and Weyl 1918).

A parallel chain of events occurred in the eighteenth and nineteenth centuries in S. Africa. First, trekboers established ranches, used them exhaustively, and then moved on. Later, trek farming arose as a transhumant system of seasonal movements between sourveld (tall grass) in summer and sweetveld (short grass) in winter (Rowland 1937). Land settlement and livestock disease put an end to the practice of trek farming; thus deferred grazing systems were developed.

Widespread changes of S. African range from grassveld to dwarf shrub and bare soil by 1950 were thought to be a result of continuous grazing (Howell 1978). A three-camp rotation system (1950-61) failed to reverse the trend, and caused patch grazing problems. Multi-camp nonselective grazing began in 1961, wherein stock were concentrated onto small areas to prevent selective grazing. Grazing bouts were short, to prevent overgrazing of regrowth.

Grazing systems were later touted as a way to increase production. Grazing systems enforce more even distribution and thereby achieve fuller utilization of the land. As water points, salt licks, and fencing are installed in stages, the landscape becomes more fully, and thus efficiently, utilized (Ares 1936a,b, Anderson 1967). Livestock can be forced to utilize less preferred forage species when they are confined in a given pasture. Management costs can be reduced because animals can be more easily controlled as tight herds (Kennedy 1963).

The benefits of grazing systems have since been called into question. Many grazing systems have had no effect and where they have, the impacts have been less significant than those resulting from simple changes in stocking rate (Van Poollen and Lacy 1979). Grazing systems proved ineffective in annual grasslands (Ratliff 1986). Grazing systems have also proven ineffective in Australia (L. Myers 1972). A large number of experiments have shown maximal animal production under simple continuous grazing (Gammon 1978, Wilson et al. 1984).

Forage quality and quantity on a short duration grazing (SDG) system were not different from quality and quantity under longer rotation systems (Heitschmidt et al. 1987a,b,c). Harvest efficiency was not improved by SDG (Heitschmidt 1987a). Recent studies comparing SDG with other grazing systems have failed to show any benefits (Pitts and Bryant 1987, Hart et al. 1988, Willms et al. 1990, Ralphs et al. 1990, Gillen et al. 1990). Many tests of SDG effects on soil properties and seedling establishment have failed to show any positive effects (Balph and Malechek 1985, Warren et al. 1986, Thurow et al. 1986, Weigel et al. 1990). Rigorous tests of SDG impact on range that is degraded, subject to patch grazing and sealing soil are lacking.

Additional confusion arises from coincident plant responses to climate. The notion that overgrazing was the original cause of a change from grassveld to dwarf shrubland (karoo) in S. Africa has little scientific basis (Hoffman and Cowling 1990). The country experienced drought during 1925-1933 and 1944-1953. Most of the theory of karoo invasion originated during 1947-1953. Thorough examination of evidence suggests that vegetation change has been influenced more by climatic change than by mismanagement (Hoffman and Cowling 1990). The effects of good rainfall from 1968-77 (Howell 1978), could have confounded the original tests of SDG. Unfortunately, there was no appropriate control treatment (Gammon 1984, cited by Heitschmidt 1987a).

Confusion and even dispute have arisen regarding plant responses to these movement patterns, suggesting that hypotheses of the

effects of herbivore movement on plants must be more explicitly stated and tested.

Traditional Pastoral Movement Patterns

It is yet more difficult to understand how ungulate movements affect plants in pastoral ecosystems. Pastoral ecosystems involve movements over large spatial scales, in poorly understood patterns. The movement patterns, or the effects of movement patterns on plants, have rarely been studied. The causes and ramifications of nomadic pastoral land use, in particular, are poorly understood (e.g., Darling and Farver 1972, Widstrand 1975). Traditional nomadic pastoralism is commonly perceived as a wandering form of land use that is devoid of any systematic management and thus prone to induce range degradation. When understood, however, nomadic pastoralism often proves to be a rational and sustainable system for exploiting rangeland plant resources.

Bedouin herders in Saudi Arabia move opportunistically among very large areas of land in response to random, patchy rainfall (Perevalotsky 1987). Forage is communally owned. It is more beneficial for a pastoral group to grant neighbors access to forage when it is available than to exclude them, as the neighbors will reciprocate. It is impossible for a single pastoral group to use all the forage on its patch of land during the brief period that it is available. Settlement of Bedouins around permanent watering points near oil-producing facilities has only promoted yearlong grazing and vegetational destruction (Heady 1972).

The Phala nomads of the Tibetan Plateau (Goldstein et al. 1990) rotate between a multipasture encampment used in winter, spring, and summer and an encampment used in fall and early winter. This system allows the nomads to utilize growing foliage during summer. It provides an ample supply of ungrazed forage reserve for use in fall and early winter, which prepares animals for subsistence through the long winter. A feudal lord (Lama) periodically reallocated pasturing rights to groups in proportion to their herd sizes.

Nomadic pastoralists in Turkana, Kenya (McCabe 1983; Coughenour et al. 1985b; Coppock et al. 1986, 1988; McCabe and Ellis 1987) are most densely aggregated during the wet season. The pulse of annual grass growth on the wet season range is brief and senescence is rapid (Coughenour et al. 1990). It is difficult for livestock to fully exploit all facets of the wet season range during the brief growing season. As the dry season progresses, the pastoralists disperse throughout the higher rainfall areas in the region. In late dry seasons, or in drought, pastoralists utilize the high mountains and plateaus where there is little water and difficult terrain. Dry season ranges are consequently rested during the growing season.

It is not exactly clear why the more productive dry season ranges of Turkana are used little in the wet season. These areas may be avoided because of cooler temperatures, which are bad for camels, and lack of mineral springs, which are good for camels. Ticks are more prevalent. But if pastoralists failed to concentrate on the less productive wet season area, a great deal of nutritious (though transient) plant productivity would be lost to decomposition, termites, and abiotic weathering. Pastoralists who move to the wet season areas would thus gain a competitive advantage. Pastoralists who remained on the dry season range year around would experience competition from the influx of pastoralists as they return from the wet season range.

The Jie of Uganda move in an opposite pattern (Gulliver 1965). Camps are widely dispersed on the wet season ranges. As the dry season progresses, the Jie shift to the west and become progressively concentrated around permanent water sources. There is intense public disapproval of those who camp on dry season ranges during the wet season as these pastures are recognized as a necessary dry season reserve.

Different dispersal-convergence movement patterns arise in response to the spatial dispersions of the most limiting resources (Baker 1978). When water is available all year, or widely distributed, then dispersal should occur during the dry season to exploit widely scattered patches of plant growth. Grazers should be concentrated on patches of favored or transient forage in the wet season. Where water is clumped in the dry season, then there should be wet season dispersal to plants that are far from water.

Pastoralists of the Niger delta of the Sahel traditionally moved into the Northern drylands in the wet season to exploit the transient pulse of plant growth (Breman et al. 1978). Overgrazing of the wet season range was prevented by movement responses to scarce water distributions. In the dry season, the herders returned to the more productive Niger delta. It would otherwise be relatively disadvantageous to remain in the delta during the wet season due to wet ground, poor forage quality, and tsetse when there is an abundant supply of high quality forage in the north.

A much larger and longer-term pattern of movement has been associated with African pastoralists. Until 4,000 years ago the only pastoralists in Africa were on the west coast of the Red Sea, but by approximately 2,000 years ago, pastoralism had spread to East Africa (Lamprey 1983). Approximately 1,300 years ago, Fulani pastoralists in Senegal were spreading east (Baker 1978). The Masai occupied northwest Kenyan lowlands (present Turkana) 400 years ago (Talbot 1972). They continued to move south until about 1640. Talbot (1972) thus hypothesized that Masai probably overgrazed their land, abandoned it and moved on fairly frequently. Lamprey (1983) also hypothesized that intra-regional movements were part of a large scale pattern of overgrazing and abandonment. However, there is little evidence that environments were actually degraded by overgrazing or that this was the cause of dispersal. Changes in climatic patterns as well as the general trend of human population growth and expansion over the continent must also be considered.

Nomadic pastoralists have been associated with the "tragedy of the commons" (Hardin 1968) syndrome. As rangelands appear to be open for free access, pastoralists would seem to have little or no personal incentive for conservation. However, it is doubtful that any pastoral system operates under true "open access" (McCabe 1990). In East Africa, for instance, forage can be used by any member of a tribe or tribal section but well water rights are owned and this limits foraging. Tribal or sectional territories are also defended from use by outsiders: evidence of a form of livestock density regulation (McCabe 1990).

Traditional pastoralism has often come into conflict with other forms of land use. Settled agriculture and other forms of economic development often restrict traditional movements or preclude the traditional grazing pattern altogether. Interestingly, when these disruptions do occur, a common result is some form of overgrazing. Thus, inappropriate pastoral livestock movement patterns are particularly likely to arise in the early stages of economic development. Economic development imposes boundaries that preclude traditional strategies of dispersal migration (Talbot 1972, Lamprey 1983). Authoritarian systems of supervised grazing management have been advocated to compensate for the inadaptation of the traditional system to the new situation (Lamprey 1983).

In the Sahel, there is a widespread pattern of localized overgrazing around developed watering areas (Sinclair and Fryxell 1985). Eventually locally degraded areas fuse across the region. When watering points are developed on wet season ranges it becomes more likely that grasses will be grazed during their growth cycle. When settled agriculture promotes year-around use of traditional dry season grazing areas, the grasses there are never rested. The inadvertent consequence is the removal of mechanisms which prevent overuse.

Development efforts in Masailand, Kenya, in the 1950's included water point development, fencing, and veterinary services (Talbot 1972). These improvements led to great increases in livestock numbers, accelerated by imports of livestock into some areas. A series of dry years occurred, culminating in 1961. Areas that were most developed, and probably most heavily stocked, suffered the most during this drought.

Group ranching, first implemented in Kenya as early as 1969, is a system wherein a parcel of tribal land is allocated to a group of pastoral households. A committee oversees its subsequent development. However, sedentarization and restrictions on cattle migration have favored increased holdings of closer-ranging sheep and goats (King et al. 1984). Livestock populations have increased in response to more watering points, better veterinary service, and large development loans. This has probably increased grazing pressures on plants and the likelihood of overgrazing after drought.

African pastoralists and open range ranchers have repeatedly rejected fenced ranching schemes (Behnke 1984). Botswana pastoralists believed that this would trap herds on ranches that were periodically untenable due to local drought, fire, or borehole breakdowns. The Masai have stressed problems of spatially erratic rainfall and periodically insufficient resources on particular ranches.

Unfortunately, economic development efforts have usually failed to calculate the effects of long-standing spatial constraints on livestock abundance and spatial distributions, and effects of movement on plant-animal interactions. Effects of developmental changes which override constraints such as water limitations on livestock distributions must be better anticipated. Developmental planners should: (1) specify appropriate stocking rates using knowledge of plant and soil responses to specific grazing regimes; (2) determine how stocking rates should vary in response to climatic variation; (3) consider the distributions of nonforage resources (such as water) on the landscape and their impacts on spatial and temporal herbivory patterns; and (4) develop options for redistributing livestock over larger spatial scales in response to changing patterns of rainfall and forage availability. It is important to consider the effects of intra-regional spatial redistribution patterns on plants in any determination of regional carrying capacity.

Wild Ungulate Movements and Interactions with Plants

The idea that wild animals move in a manner that conserves forage and prevents overgrazing can be traced at least back to Smith's (1895) reference to bison. More recently, Bell (1978) recounted that bison and wild horses migrated, by coincidence, in a pattern that was beneficial to both plants and animals. Summer elk grazing has been likened to a complex deferred rotation grazing system in which plants grazed one year may go unused in following years (Gruell 1973, cited by Houston 1982). However, the idea that migratory movements would evolve to conserve forage would probably not be accepted by evolutionary theorists because it would require altruistic sacrifices by individual animals. This does not rule out the possibility that other proximal causes of migration (such as patchy rainfall and snow distributions) might create a situation in which forage is conserved, however.

In most regions bison moved nomadically in response to variable local and regional rainfall patterns. Although bison movements were highly erratic, large-scale patterns were observed in some regions (Roe 1951). Southern herds generally moved north in summer to escape heat. Some herds were observed to utilize eastern grasslands in the spring because they initiated regrowth before western grasslands. Canadian herds moved north in winter into the scrub belt for shelter and south onto the plains in summer. Thus, extreme southern grasslands were probably little grazed in mid-

summer. Many eastern grasslands could have not been grazed in summer while many western grasslands could have avoided herbivory in the early spring. Grass in the north Canadian scrub belt would have been rested in the summer. Erratic movements at small and large scales would have imposed a deferred rotation in that a given area would not likely be grazed at the same time every year. Return movements would have taken time, thus providing deferment during early season regrowth.

Saiga antelope in southwest Asia are essentially nomadic but they also move regularly between summer and winter ranges (Bannikov et al. 1967). Summer and winter range distinctions are blurred in mild winters. Summer movements are mainly responses to unpredictable rainfall patterns while winter movements are responses to snow distributions. Movement and searching would give some grasslands a chance for regrowth. Productive grasslands of lakeshores and riverbanks areas are apparently avoided during good years. This is fortuitous because these areas then act as dry season grazing reserves.

Wildebeest in the Serengeti (Pennycuik 1975, Inglis 1976) and the Kalahari (Williamson et al. 1988) and kob in southern Sudan (Fryxell and Sinclair 1988) make long-distance treks to areas of low annual rainfall at the beginning of the wet season. These are areas where grasses are typically shorter in stature and available for only a short period of time. Serengeti short grasslands are probably favored over taller grasslands because soils and plants are much richer in mineral nutrients (Kreulen 1975, McNaughton 1990). Mineral pans in the Kalahari wet season area are used as licks prior to calving (Williamson et al. 1988). Forage quality of taller grasses is also inherently lower than that of short grasses due to a higher degree of lignification.

What explains the low number of resident ungulates in the higher rainfall areas of the Serengeti? It would seem these productive areas could support many more grazers during the wet season. A few resident herds of wildebeest and many water buffalo stay on the more productive area year around, but clearly they do not exploit all the forage that is available to them. Migrants gain access to a transient, though expansive and nutrient-rich, resource on the shortgrass plains. Migrants consequently would increase in number relative to residents. The migratory strategy would increasingly prevail over the resident strategy. At the end of the wet season when the huge herds of migrants return to the taller grasslands they remove large quantities of forage, to the disadvantage of the residents. Competition from large numbers of returning migrants at the height of the dry season (Sinclair 1983) would also reduce numbers of residents. The ratio of residents to migrants should be dictated by the ratio of net benefits of each strategy (Sinclair 1983).

The exodus of migrants provides a period of rest for grasses in the more mesic areas in the wet season, although certain areas are heavily grazed by residents, even forming grazing lawns. During the wet season wildebeest and other ungulates chase patchy rainfall and waves of nutritious regrowth on the shortgrass plains (McNaughton 1985, Durant et al. 1988). Possibly, shortgrasses exhibit a short burst of intense production before they are "discovered", but wildebeest have been noted to arrive at areas of rainfall within three days (McNaughton 1985). At the end of the wet season tremendous "grazing fronts" pass through transition grasslands dominated by *Themeda triandra* and other midgrasses. Spatially separate short grasslands lure herbivores away from the transition grasslands during the growing season by virtue of higher plant nutrient content and reduced predator danger. *T. triandra*, a grazing sensitive species, consequently thrives in the presence of the large free-ranging herbivore population (Coughenour et al. 1985a).

When Wildlife Movements are Disrupted

Fencing has negatively affected wild ungulate numbers in the

Kalahari. Wildebeest have declined due to restricted migration to surface water (Williamson et al. 1988). One of three subpopulations of wildebeest in Kruger National Park declined after fencing restricted access to summer grazing areas (Whyte and Joubert 1988). Large herds initially built up on the remaining summering area within the fence. This resulted in overgrazing and the herd was consequently culled. A second fence was erected to exclude animals from the overgrazed area. Now, only sedentary animals remain on scattered patches of suitable habitat.

In contrast, ungulate overabundance and overgrazing in wildlife preserves has also become a serious problem. It often appears that animal populations are confined or compressed and that their dispersal is prevented (see Caughey 1976a), but this is often against a background of declining populations outside reserves.

Presumably, ungulates normally disperse in search of better conditions when forage supply is reduced by drought or grazing. According to the compression hypothesis, regional scale systems of movement that are necessary for system persistence are disrupted by humans, thus causing ecosystem degradation (Cahalane 1943, Buechner and Dawkins 1961, Pengelly 1963, Lamprey et al. 1967, Laws 1969, N. Myers 1972). Long life spans of large herbivores could prevent rapid readjustment of the compressed population to its food supply if the compression occurs abruptly.

For example, there has been historic concern that there are too many elk on Yellowstone's northern winter range because movements out of the park have been restricted (Cahalane 1943, Pengelly 1963, see Coughenour and Singer 1991). Land areas north of the park have been occupied by ranches and agriculture, and it seems clear that hunting pressure outside the park could suppress emigration. Aside from the lack of firm evidence, the situation is not this simple. If elk regain access to ranch and farmland, as they now are, it seems reasonable to expect that the population will increase in response to a greater forage base. Elk numbers would likely increase if hunting were eliminated. A mechanism must be proposed that would force elk off park areas that have ample forage. One possibility is that greater snow depths within the park would drive elk downhill, particularly in severe winters. Yet, elk have historically coped with snow depths on the park's winter range.

Much controversy arose over elephant in Tsavo National Park, Kenya, in the 1960's and early 1970's (Laws 1969, Glover 1972, Sheldrick 1972, N. Myers 1972, Croze et al. 1981). Elephant numbers had gradually increased within the park under a policy of no culling. Substantial numbers of elephant likely immigrated into the park during 1960–70 (Corfield 1973). At the same time, dispersals were thought to have been inhibited by human populations surrounding the park. A drought occurred in 1970–1971. Due to lack of browse in proximity to water, many elephants died from starvation (Corfield 1973).

Tree populations declined considerably between 1970–74 (Leuthold 1977), which was attributed to elephant damage. Yet, bone isotope composition indicates that browse was not used more heavily during drought (Tieszen et al. 1989). Possibly, elephant were highly dependent on annual browse growth, which was reduced by the drought. As a result, elephant may have harvested accumulated browse standing crop. The relative effects of drought and browsing, and their interactive effects on woody plants, have not been clearly distinguished.

The elephant die-off was perceived to be a result of overpopulating and over-browsing (N. Myers 1972). Blame for the die-off was placed on the interference of humans with natural elephant dispersal patterns. It was asserted that elephants historically migrated to alternative grazing areas when drought, or their own utilization, reduced the local forage supply.

Possibly, rainfall patterns in this region are patchy at the scale of

elephant movements, which would induce a large-scale shifting mosaic of plant growth. This could promote plant-herbivore stability. As spatially separated resource levels vary nonsynchronously, then time required for searching and movement among these areas would provide time for plant regrowth. Studies of elephant movements after the 1970–71 drought in Tsavo (Leuthold and Sale 1973) demonstrated that elephant move over long distances during the wet season in response to changes in the distribution of rainfall and resultant vegetation growth. However, studies have also suggested the possibility of spatially fixed dry-season ranges. Nearly all of the mortality during the 1970–71 drought occurred in dry-season concentration areas near rivers in the more arid half of the park (Corfield 1973).

Possibly there are ecological or evolutionary advantages of dispersing to marginal habitats or "sink areas" (Owen-Smith 1981). Natural selection could favor competitive exclusion or territoriality that would force surplus animals to disperse to less favorable habitats before overgrazing occurs.

The phenomenon of fencing-induced population increases has been called the Krebs effect (MacArthur 1972, Krebs et al. 1969, Stenseth 1983). Krebs et al. (1969) observed a population of field mice increased to unnatural densities within a small fenced area until food eventually limited population growth. This effect has not yet been explained, although it has been theorized that fencing may override a natural tendency towards intraspecific aggression and consequent dispersal (Stenseth 1983).

Application of a frustrated dispersal hypothesis to ungulates in parks requires that several difficult questions about traditional movement patterns be answered. To where would ungulates have dispersed? What level of forage or population density would trigger the dispersal? Would the trigger have been conservative enough to prevent overgrazing? Why? In some cases suggested dispersal sinks are actually areas of ample resources. Why would such habitats be underutilized? Functional relationships between dispersal, competitively controlled density, and relative plant availability are very poorly known.

Good explanations of overabundance and overgrazing in wildlife preserves require much better analyses of the spatial component of the plant-herbivore system. Synthetic quantitative analyses of climatic driving variables, herbivore movements, plant responses, and system dynamics are needed. While experimentation provides the strongest support, this is difficult or impossible at these very large spatial and temporal scales.

The Importance of Scale for Analyses of Plant-Herbivore Interaction

Specific ecological interactions are limited to specific domains of scale (Senft et al. 1987, O'Neill et al. 1988, Weins 1989, Kotliar and Weins 1990). Complex problems can be decomposed into more manageable pieces by identifying which plant-herbivore interactions occur over which spatial scales. Problems of confusing causes at one scale with responses at another are also avoided.

Although grazing may appear to be relatively uniform at coarse levels of resolution, this may only be because significant pattern at finer scales is blurred. In reverse, apparently uniform grazing can actively comprise a patch of grazing at larger landscape or regional scales.

Hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) states that the details of finer scale processes at lower levels of organization become insignificant at higher levels of organization: only the emergent behavior of the fine scale processes is significant at larger scales. Conversely, processes at higher levels of organization change too slowly or vary over too large a spatial scale to be perceptible at lower levels; yet the large scale provides the context within which the finer scaled system must operate.

Perceived plant response to herbivory depends on the scale and level of organization at which the response is measured (Brown and Allen 1989). Detrimental grazing impacts on plants are more likely to be measured at smaller spatial and temporal scales. Over a period of several days or several weeks grazed plant growth can prove to be less than ungrazed plant growth. Over a year, however, the grazed plants could compensate for their losses because limiting nutrients are recycled at a faster rate by herbivores (e.g., McNaughton 1979, 1984; Coughenour 1984; Ruess and McNaughton 1984; Detling 1988). Water to support regrowth may be retained in the soil. If a single plant is defoliated in a patch of 3 plants, the patch response is not necessarily simply one-third of a typical defoliated plant response plus two-thirds of a typical non-defoliated response. The 2 nondefoliated plants in the patch can grow at a faster rate due to defoliation of their neighbor and reduced competition for limiting resources (e.g., Mueggler 1972).

The landscape scale plant response to herbivory cannot be assumed to be equivalent to an average grazing pressure that is applied continuously and uniformly to an average plant. The aggregate response of a sward that is uniformly defoliated by 50% can be quite different from the aggregate response if 50% of the plants are 100% defoliated. If grazing is highly patchy, it will be unlikely that any plant will have experienced the fictitious average of grazed and ungrazed patches. Thus, individual plant responses can only be translated to the landscape scale response by incorporating information about patch and community scale patterns.

Grazing Patterns at Tiller, Patch, and Community Scales

Herbivory patterns at tiller through patch scales cause unique responses at higher levels of organization. Two types of patch scale patterns in particular cause ecosystem responses that would not occur if herbivory was spatially uniform: grazing lawns and patch grazing.

Grazing lawns are an alteration in plant form and function in response to frequent close grazing, characterized by a drastic reduction in height and activation of an increased number of tillers with few short stems and more horizontal leaf angles (Vesey-Fitzgerald 1973, McNaughton 1984). Forage quality is usually greater on a grazing lawn than off.

It has been hypothesized that grazing lawns are a unique benefit of herd formation (McNaughton 1984). While an individual animal could form a small grazing lawn, it would be more susceptible to predation (Estes 1974). In a dense herd animals have few opportunities to be selective, particularly when the herd is moving slowly. This imposes relatively uniform grazing intensity. Competitive advantage normally afforded to nonpreferred plants or tillers is consequently eliminated. Therefore, herds are more likely than individual animals to exert consistent grazing pressures required to shift dominance towards lawn forming species or genotypes. Ungulates probably have to move as herds to form large lawns. But when they do so, the nutritional advantages of feeding on lawns may be offset by lower intake rates (Hobbs and Swift 1988).

When forage quality is greater on grazed areas, total nutrient flow to herbivores can be accelerated even when total net primary production is lower. This has been documented, for example, on prairie dog towns (Jaramillo and Detling 1988). Grasses on young dog towns have more prostrate morphologies (Detling and Painter 1983, Jaramillo and Detling 1988) and higher rates of nutrient uptake (Polly and Detling 1988, Jaramillo and Detling 1988). This could be why these areas are used preferentially by bison (Coppock et al. 1983).

Patch grazing (Stobbs 1970, Bakker et al. 1983, Ring et al. 1985) is initiated when forage supply exceeds demand (Spedding 1971). Regrowth on grazed patches becomes higher in quality than the surrounding ungrazed matrix. As time passes grazers continue to

select the regrowth and the grazed patches diverge further from the ungrazed matrix in terms of forage quality and plant form, and a mosaic pattern develops in the pasture. It has been hypothesized that patches form a dynamic mosaic, with grazed patches being formed from nongrazed patches of previous years. While patches persist for 4 or more years (Willms et al. 1988), use of grazed patches has been shown to decay over time (Hobbs et al. 1991). While net primary production on grazed patches is sometimes lower than that on ungrazed patches, there are more available nutrients in the soil of grazed patches (Willms et al. 1988). Ungrazed patches provide emergency forage in years of poor rainfall (Willms et al. 1988).

Patch grazing can lead to ecosystem degradation (Mott 1987). Once selective grazing of patches begins, continued grazing pressure can lead to rapid death of individual plants. Areas of plant death form "scalds", which result from soil surface sealing (Bridge et al. 1983). Removal of the vegetation and litter cover exposes the soil to direct raindrop impact. In soils of intermediate texture the raindrops can deflocculate soil aggregates, glance off finer soil particles and deposit them in the form of crusts on the soil surface (see Shainberg and Singer 1985). Also, reduced carbon inputs to the soil can accelerate degradation of soil structure (Mott et al. 1979). In subsequent seasons new patches are formed, expanding the degradation. Dry-season fires can be used to remove the patches, thus increasing the stability of the pasture as a whole (Andrew 1986, Coppock and Detling 1986, Hobbs et al. 1991).

Importantly, large scale movements of grazers in grazing systems impose particular smaller scale patterns of defoliation among individual tillers. Continuous and rotation grazing system effects on tiller-scale defoliation patterns were compared by Gammon and Roberts (1978). Under continuous grazing some tillers were repeatedly utilized (thus showing a tendency towards patchy grazing at tiller scales). Intermittent grazing reduced the number of tillers that were defoliated three or more times. A greater percentage of tillers was grazed under a heavier stocking rate (Briske and Stuth 1982). In a short duration rotation system, higher stocking rate also increased the percentage of tillers regrazed at least 2 or 3 times (Pierson and Scarneccia 1987).

When livestock were rotated more rapidly among 8 pastures, they defoliated a smaller percentage of the tillers in a given area in each grazing episode (Gillen et al. 1990). Rotation rate had no effect on the cumulative number of tillers that were defoliated over a season, but faster rotation increased the number of tillers that were defoliated repeatedly. When stocking rate was increased under a given rotation rate, a greater percentage of tillers was grazed repeatedly, and tillers of the more preferred species were grazed to a lower height. Here, duration was shortened by faster rotation of a fixed number of animals among a fixed number of pastures so rotation rate was not confounded with altered herd density. Usually when SDG is implemented, grazing duration is shortened by increasing the number of pastures, which also increases herd density. The results suggest that if higher stocking rates can be supported under SDG, as often claimed, it is likely a result of greater herd density and fuller use of available tillers, rather than a result of altered duration.

While paddock scale grazing systems are imposed to achieve a certain grazing regime, livestock may create smaller scale grazing systems of their own within paddocks. Consequently, the grazing regime experienced by plants is not necessarily predictable solely from rate and intensity of herbivore rotation among pastures. Obviously, livestock movements are not controlled under continuous grazing, but individual animals or groups can nevertheless rotate. Theoretically, any system of movement that can be implemented by fencing can be implemented by the livestock themselves (Spedding 1970). Livestock move, and they cannot occupy the

entire area all at once. They may form a concentrated area of grazing or they may create numerous scattered grazed sites (Spedding 1970). Of course, the more intensely animals are managed, the less likely it is that animals will be able to create their own small-scale grazing system.

If grazing ungulates do impose deferred rotation or short duration grazing patterns of their own within pastures, then the need for grazing systems cannot be argued on the basis of a need to rest plants. Rest is provided by livestock movements within pastures. Unfortunately however, the natural grazing system of the animals is often in balance with plant growth at an undesirably low stocking rate: livestock may only prefer to use parts of the landscape, some of the patches or some of the plant species.

The Need to Consider Landscape Physical Constraints on Ungulate Distributions

Analyses of spatial plant-herbivore interactions requires knowledge of physical constraints upon ungulate distribution on the landscape. Spatial distributions of landscape physical factors, climate, and herbivores can be used to estimate spatio-temporal patterns of herbivory and plant growth. Patterns of herbivory on the landscape are constrained by spatial distributions of topography, cover, water, and minerals. Effects of habitat structure on wild and domestic ungulate distributions have been documented in a great number of studies. A sample of these is provided here to illustrate their potential effects on spatial patterns of herbivory.

Topographic effects can be broken into five different types: (1) effects on herbivore movement and foraging; (2) effects on microclimate experienced by herbivores, (3) effects on interactions with predators; (4) effects on social grouping; and (5) effects on plant growth.

Topography affects movement by either imposing physical barriers or by increasing the time and energy required to move a certain distance. Slopes can simply be too steep for travel. For example, cattle avoid slopes of greater than 30% and horses avoid slopes greater than 50% (Ganskopp and Vavra 1987). Elk spend far more time on gentle than on steep slopes (Houston 1982). Slope amplifies other distance functions. The costs of travel to water are increased on steeper slopes such that vertical distance above water affects cattle distributions (Roath and Krueger 1982).

Topography defines movement pathways across the landscape. For instance, landscape form determines the locations of cattle trails (Weaver and Tomanek 1951, cited by Arnold and Dudzinski 1978). Use of plants on the landscape is influenced by their proximity to these trails. Regular deer migration routes are often along corridors defined by topographic features such as ridges and canyons (Thomas and Irby 1990), with preferential foraging in open areas along the route. Locations of mountain passes affect the accessibility of entire landscapes and the use of plants within those landscapes.

Regional topographic characteristics have had an influence on the geographic distribution of bison (Van Vuren 1987). Much of the terrain west of the Rockies is a disjunct mosaic of habitats separated by physiographic barriers to movements such as mountains and canyons. This inhibited movements of local populations out of areas which are periodically impacted by drought, heavy snow, or predation. Over time, resultant local extinctions depressed the regional population, which may in turn, have affected the coevolutionary relationship between herbivores and plants (Mack and Thompson 1982).

Topographic influence on snow depth affect ungulate movement and foraging. Winter ranges of horses in some areas are characteristically on or near wind-swept ridges (Miller 1983). Wind-blown ridges are important snow-free areas for pronghorn (Ryder and

Irwin 1987) and elk (Houston 1982). Elevation effects on snow depth determine the sizes and configurations of elk winter ranges (Houston 1982, Wambolt and McNeal 1987).

Topography affects the microclimate that is experienced by animals through effects on orientation to sun and prevailing winds, as has been demonstrated for cattle (Senft et al. 1985b) and wintering pronghorn antelope (Ryder and Irwin 1987). Pronghorn prefer habitats with sites that provide shelter from prevailing winds and sites that are warmed by the sun.

Topography provides escape from predation for ungulates that can exploit rugged terrain (Krausman and Leopold 1986). Bighorn move to their summer range long before good forage is present, apparently to find terrain needed for predator avoidance during lambing (Festa-Bianchet 1988). Mountain goats and other caprids also use topography for predator avoidance (Hutchins and Geist 1987).

Topography affects social grouping and home range formation. Distinct cattle groups used different parts of a mountainous rangeland (Roath and Krueger 1982). This was suggested to have been due to the influence of visual and topographic barriers which increased social links between individual animals in a group.

The distribution of physical vegetation structure is another habitat variable having widely recognized effects. Habitats containing adequate quantities of vegetation cover are often preferentially utilized. Shrub cover is important for elk (McCarquondale 1987) and deer (Wambolt and McNeal 1987). Dorcas gazelle in Africa require streambeds lined by shade-providing *Acacia* trees (Babarav 1982). Kangaroos prefer areas with protective cover (Terpstra and Wilson 1989). Gregarious ungulates avoid wooded cover. Cattle are seldom seen in small grassland openings, possibly because the openings are too small to support a complete herd (Pratt et al. 1986).

The effects of water distribution are well known (e.g., Ares 1936b, Western 1975), but they are infrequently quantified. Water availability can be more limiting than forage for African ungulates (Western 1975, Williamson et al. 1988). Recent studies have demonstrated: the extent to which water affects cattle land use on Oregon mountain rangeland (Roath and Krueger 1982); that summer horse ranges tend to be within 4.8 km of water (Miller 1983); and that water determines dry season kangaroo distributions (Low et al. 1981).

Mineral licks have well-known effects on ungulate distributions (Ares 1936a, Jones and Hanson 1985, Krueken 1985). The spatial distributions of forage mineral contents are seldom considered, however. Ungulate foraging habitat preferences in the Serengeti are highly related to the mineral contents of plants, which in turn, are related to mineral contents of soils (McNaughton 1988, 1990). Soil nutrient levels significantly affect the distribution of ungulate carrying capacities at regional scales (Bell 1982, East 1984).

Models of Herbivore Movements and Distributions

An early quantification of the relationship between ungulate spatial distribution and landscape factors was Cook's (1966) use of multiple regressions to explain livestock spatial utilization patterns. Regression equations were later used to model ungulate distributions over an entire landscape (Senft et al. 1983, 1985a, 1985b). Topographic factors at each position on the landscape were used as input to the regression model. A regression approach was used to analyze winter elk foraging sites (Grover and Thompson 1986). Relationships with single variables such as distance to cover, distance to road, and forage density were noisy. However, a significant portion of the variance was explained by combinations of variables. Favorable combinations were in short supply on the landscape. Average distribution of sheep in an Australian pasture was modeled with a multiple regression equation that included

terms such as inverse squared distance to water, linear distance to shade, linear vegetation preference, and presence/absence of fence (Smith 1988). Continental scale distributions of kangaroos in Australia were modeled from a number of climatic variables (Walker 1990).

Multiple regression analyses have some limitations. They usually do not consider interactions among variables. They are usually static; otherwise separate models must be constructed for different seasons (e.g., Senft et al. 1983, 1985b).

These limitations have been overcome in the technique of habitat suitability index modeling (Schamberger and Krohn 1982, Cook and Irwin 1985). Habitat suitability index modeling is part of the general Habitat Evaluation Procedures (HEP) developed and used within the U.S. Fish and Wildlife Service. A first step in this procedure is to use simple correlation and multiple regression to identify habitat variables that are correlated with ungulate densities and measures of reproductive success (Irwin and Cook 1985). Sampling is conducted over a wide range of conditions. Individual suitability index functions are then constructed for the most explanatory variables and these functions are combined together into an equation for the habitat suitability index. Ideally, animals would be distributed in proportion to habitat suitability.

The ideal free distribution described by Fretwell (1972) assumes an equilibrium wherein additional movements cannot improve resource availability to any animal. Ideal free assumptions are implicit in regression models as well as habitat matching rules (Herrnstein 1974, Pulliam and Caraco 1984, Fagan 1987) and optimal foraging models, in which the relative numbers of individuals using different habitats perfectly match resource availabilities. Matching models are based on the assumption that competition among individuals brings about an efficient spacing of individuals in relation to biotic and abiotic resources. Optimal foraging theory assumes ungulates have perfect knowledge of forage distribution.

The assumption of a static equilibrium can be partially surmounted by recalculating the distribution as the landscape changes. A dynamic model of sheep distribution was formulated based upon a water balance equation, which was affected by seasonally and spatially varying evaporative demand and vegetation condition (Smith 1989). In another dynamic application (Coughenour 1991a, 1991b), a habitat suitability index was calculated on a weekly to monthly interval for each spatial grid cell of a simulated regional pastoral ecosystem. The index incorporated functional responses to temporal variations in forage abundance due to rainfall variation, prior grazing, and loss of forage to litter and abiotic weathering as well as functions for static effects of water, topography, and cover.

As competitive interactions among individuals are weak or non-existent in variable and harsh habitats, density distributions are more prone to be random (Weins 1984, 1985). Imprecision is inevitable when attempting to explain individual animal locations at fine spatial and temporal scales. However, the random noise at fine scales can be averaged out over longer time periods so that the mean distribution does approximate the distribution of resources on the landscape, irrespective of competition.

Mismatching between dynamic animal and resource distributions arises when movements are slow in comparison to rates of environmental change. Animal movements must be explicitly treated to address this type of problem. One approach is to consider the movements of animals in space as a diffusion process (e.g., Taylor and Taylor 1977, Okubo 1980). The migration model of Taylor and Taylor (1977) included immigration and emigration rates as functions of density. The model was applied to a time varying random mosaic of cells having 1 of 3 habitat qualities. Movements became a game of hide and seek, with net distribution reflecting "the balance between rates of environmental change and

the movement and reproductive rates of the organism, which fails to use some resources because they are not discovered in time" (Taylor and Taylor 1977).

Time required for population growth also poses problems for the equilibrial assumptions of an ideal free distribution. Hobbs and Hanley (1990) used simulation modeling to show that distribution among habitats also depends on the relative positions of local populations along their growth trajectories, and random disturbances in those trajectories. A mismatch of density and resource abundance can arise, for example, from a dramatic reduction in population density due to locally catastrophic weather. Slow immigration and population growth would cause the mismatch to persist for a significant period of time. Empirical "snapshot" distributions cannot be assumed, therefore, to reflect relative carrying capacities.

Individual habitat selection is not likely to be optimal (Weins 1984, 1985). In reality, individuals lack perfect knowledge of the distribution of resources in the environment, particularly when the distributions are changing stochastically. At any given point in time, populations are unlikely to be spaced in perfect proportion to resource abundance. Movements are sometimes made impossible or they are significantly impeded by barriers (Weins et al. 1985).

Limitations of aggregate population models are a consequence of the simplifying assumptions about the mean behavior of the population. Individual organisms interact with their immediate local environments; and these local environments are heterogeneous in space and time. An individual based modeling approach (Huston et al. 1988) avoids many of the simplifying assumptions that are required when these heterogeneities are ignored. Predictions of individual based models will be different than predictions of aggregate models if heterogeneity at small spatial scales promotes unique processes—and especially if those processes involve positive feedback (Huston et al. 1988).

The actual mechanisms of animal foraging are considered in an individual based approach. Individual based movement models that have been constructed (e.g. Siniff and Jessen 1969, Owen-Smith and Novellie 1982, Saarenmaa et al. 1988, Folse et al. 1989) have proven very useful for explaining foraging patterns and efficiencies. For example, one group (Senft et al. 1987) constructed a rule-based model of individual ungulate foraging. The model has proven useful in classroom exercises to demonstrate net effects of fine scale foraging behavior within and among feeding stations on total intake over one or more foraging bouts (L. Rittenhouse and D. Swift, pers. comm.).

Unfortunately, the behavioral rules that govern individual foraging behavior are poorly known. To elucidate these rules, individual animals must be subjected to carefully controlled environments such as the mazes used in animal psychological research. Using such an approach, Bailey et al. (1988) have found that cattle tended to follow a win-switch strategy, as individuals moved after discovering productive patches. Cattle tended to return to productive areas more often, which suggested spatial memory (Bailey et al. 1987).

A serious limitation of individual based models is the computational demand required to represent large numbers of animals over large areas. For example, it would be highly impractical to apply an individual-based approach to model 10,000 pastoral herdsman and their livestock in over a 10,000-km² area in southern Turkana, Kenya. Consider that the interactions of each herdsman with many neighboring herdsman would have to be simulated to represent population distribution.

Both individual based and aggregate models have advantages and disadvantages. To a large extent the appropriate model depends on the spatial and temporal scale of the questions that are to be answered. However, a two-way flow of information among

both approaches would be optimal, to understand ungulate use of space over a wide range of scales.

Modeling Plant Growth Response to Spatial Herbivory Pattern

The salient question here is how plants respond to different spatio-temporal patterns of herbivory. Given herbivore movement responses to landscape variables, including forage quantity and quality, grazing regimes imposed upon stationary plants can be deduced—ie. the frequency, intensity, and seasonality of defoliation. Knowledge of plant responses to various defoliation regimes can then be used to predict responses to the pattern of herbivore movement.

As an example, a detailed model was formulated to explain graminoid responses to herbivory in the Serengeti ecosystem, Tanzania (Coughenour et al. 1984a, Coughenour 1984). The model was subjected to factorial combinations of grazing height and frequency (Coughenour et al. 1984b) and results were portrayed as response surfaces of plant production. Short grasses yielded most when grazed at low heights every 24 days while tall grasses responded more favorably to a longer grazing interval of about 55 days. Tallgrass was relatively insensitive to grazing heights below 16 cm. In actuality, migratory Serengeti wildebeest graze short grasslands to a minimal height, moving about the plains in 2-week (Vesey-Fitzgerald 1973) to 4-week (Sinclair 1977) rotations. The herds spend less time in any given area of the tallgrass region (Maddock 1979). According to the model response surfaces, short-grass yields would be near maximal under the observed regime. Tallgrass yields would be high, but less than maximal.

Consequences of spatial plant-herbivore interactions in rotation systems were modeled by Noy-Meir (1976). At moderate stocking rates short cycle rotation grazing had little effect on productivity compared with continuous grazing, while intensive (long cycle or many paddock) rotation depressed production. Intensive rotation substantially increased productivity at high stocking rates. When initial range condition was poor, intensive rotation increased production relative to continuous grazing. When initial range condition was good, continuous grazing was more productive. Intensive rotation at low stocking rate caused herbivory to deplete vegetation below the critical level where plant growth rate and consumption rates are equal. Rotation was more favorable on the poor condition range because of the low initial plant biomass. Rest periods were provided for vegetation to escape above the critical point where growth and consumption rates were equal.

Senft (1988) simulated spatially interactive short duration and continuous grazing systems. Herds were moved among 10–16 paddocks. SDG decreased forage production, but increased the fraction of available forage that was utilized.

A spatial model of ungulate movements and plant growth was formulated and parameterized for the Serengeti, Tanzania, migratory and Turkana, Kenya, nomadic pastoral ecosystems (Coughenour 1986). In this model shoot and root growth rates and death rates responded to stochastic rainfall patterns. Grid cell size was scaled to ungulate density to simulate a single herd at observed densities.

There proved to be little difference in Serengeti short-grass root mass between continuous and rotation grazing at moderate animal densities ($\leq 300 \text{ km}^{-2}$). At higher densities, shortgrass could only persist under a long (60 day) rotation system, but forage intake rates were too low to support the population. The Serengeti mid-grass could not withstand densities above 200 km^{-2} without a larger ungrazable reserve or a rotation cycle. A herbivore density of 400 km^{-2} was sustained with a 240-day rotation among six cells.

The standard Turkana movement pattern was a concentration onto about one fourth of the total area during the wet season,

followed by increasing dispersal among cells as the dry season progressed. This movement pattern was compared to an even, stationary livestock distribution, a regular rotation scheme, dispersion during the wet season, and a pattern where the entire population was moved to the adjacent most resource rich cell at 2-week intervals. Dry season dispersal allowed more plants to persist after 10 years because livestock were densely concentrated only during periods of high plant growth rate. Regular rotation and wet season dispersion reduced perennial plant tissue by one third. Movements to the best adjacent foraging area reduced plant density the most. Other movement patterns reduced perennial plants to very low levels in areas where initial plant density was low. Fixed rotation forced overly high densities into single cells during critical plant growth periods.

Spatial Plant-Herbivore Systems and Spatial Predator-Prey Systems

Theoretical studies of spatially distributed predator-prey systems are relevant here because they explain how spatial heterogeneity can affect system stability. A hypothesis that excited much theoretical work in the 1970's was that spatial heterogeneity can stabilize predator-prey systems and promote their persistence. Specifically, heterogeneity could prevent predators or (herbivores) from overexploiting their prey or (forage).

Both ecosystem spatial heterogeneity and size can increase stability. Thus, orange mites and their predators were more likely to coexist in environments comprised of larger numbers of oranges (Huffaker 1958). As the sizes of flasks containing microbial predator-prey system were increased, prey became more difficult to find at low densities (Luckenbill 1974). Predators were unable to search out low numbers of prey in a large volume in a short period of time; thus prey could recover while predators searched. Host trees were camouflaged from spruce budworm attack when they were intermixed with nonhost trees (Morris 1963), due to physical barriers to predator dispersal (Murdoch and Oaten 1975). Patchiness in a predator-prey system draws predators away from areas of low prey abundance, effectively forming a prey refuge (Hassel and May 1973). The stability of the system is thus enhanced. Several other modeling studies have supported this hypothesis (Hilborne 1975, Myers 1976, Ziegler 1977).

The positive effects of spatial heterogeneity on predator-prey stability can be quite important for plant-herbivore ecosystems (May and Beddington 1981). Presumably, the stability promoting mechanism would be patchy aggregations of herbivores rotating amongst a shifting mosaic of vegetation patches in various stages of recovery from herbivory damage. If so, problems of herbivore overabundance are especially likely in wildlife reserves which are too small to support a stable patch dynamic system.

Conclusions

It becomes ever more important to understand the spatial components of plant-herbivore interactions as human and ungulate uses of space intensify. Conflicts between human and ungulate land use increase as the human population grows and expands. Space becomes more limiting, wildlands are fenced off, and open rangelands are parceled out or converted to settled, irrigated agriculture. Wild ungulates are forced into smaller spaces and livestock numbers continue to increase.

Spatial components of plant-ungulate interactions underly domestic livestock grazing systems, pastoral land use practices, and native ungulate ecosystems. The sustainability and persistence of these ecosystems over the long term are strongly affected by links between spatial pattern and process. However, the linkages are unclear in all 3 types of ecosystem.

Early rotation grazing systems were patterned in design and in concept, after movements of free roaming native ungulates. Such an analogy would be much easier to support scientifically if the spatial components of herbivory were better understood. In actuality, natural movement patterns of wild ungulates in relation to plant growth are not well known and many tests of rotation grazing systems have failed to show any clear advantages.

The degree to which overgrazing in traditional pastoral ecosystems is prevented by landscape limitations on forage use is potentially high, but little understood. Pastoral development efforts must consider the ramifications of patchy rainfall over large areas and traditional movement responses to these spatio-temporal patterns. The extent to which such movements might limit population size, prevent localized overgrazing, prevent local extinctions, thus stabilizing the plant-herbivore interactions as well as the pastoral population, is not well understood. Yet much evidence suggests that spatial heterogeneity is important for pastoral ecosystem persistence.

Ecologically sound management of spatially extensive wild ungulate ecosystems demands a particularly high level of understanding of natural spatial plant-herbivore interactions. It is often difficult to provide irrefutable support for hypotheses that disruptions of natural dispersal movements cause overgrazing. Total support requires knowing the manner in which dispersal rates and patterns vary in relation to population density and forage abundance.

Carrying capacity can be variable or unpredictable in space just as it can in time (Weins 1977, Ellis and Swift 1989, Westoby et al. 1989). Density-independent periods of resource "bottlenecks" clearly exert significant limitations on populations in variable environments (Weins 1977). Spatial distributions of multiple resources also limit the spatial component of population abundance, thus creating resource bottlenecks in space.

These limitations of nonforage resources on ungulate distributions and their impacts on plants are poorly documented. Water, topography, minerals, and other resource distributions influence carrying capacity as well as plant-animal interactions. Areas of the landscape which are avoided because of inadequate nonforage resources can provide important refugia for plants. Landscape constraints then determine the minimum ungulate density which can persist through drought. The joint distribution of water and forage on the landscape during drought determines the area and thus the quantity of forage that is available. A limited, predictable number of ungulates would be supported by this area. This would suggest a form of density dependence that has been little investigated. The ability of spatio-temporal bottlenecks to support limited populations would have an important effect on the long-term carrying capacity of the landscape.

While wild ungulates cannot usually fully utilize landscapes, production-oriented systems attempt to sustainably extract as much from an ecosystem as possible. Wildlife distributions are often limited by localized deficiencies of water, minerals, and navigable terrain. Production livestock systems attempt to remove these landscape constraints by manipulating resources or animal behavior. In both cases, nonforage constraints significantly alter the plant-herbivore balance.

Experiments and models of predator-prey interactions in spatially diverse environments suggest that movements might also stabilize plant-herbivore systems. However, there are few, if any demonstrations of this concept for large herbivore populations. Herbivores should tend to move away from areas of low forage abundance, thus providing forage refugia. Patchy and unpredictable rainfall cause localized forage depletions which stimulate movement. The large scale disturbance mosaic could be stable in the aggregate. The time required for ungulate movement and

search provides opportunities for plant escape from herbivory. Ironically, stability should arise from unpredictability.

Spatial interactions and processes in ungulate ecosystems must be better known. The problems of spatial plant-herbivore interactions of today are more critical, and often more complex than those confronted by humans decades, hundreds or thousands of years ago. Failure to consider the spatial components of herbivory in carrying capacity calculations and assessments of ecosystem persistence can contribute to overgrazing, failed economic development efforts, and declines of wildlife populations. Technologies such as spatial simulation modeling and geographic information systems now exist which make analyses of spatial plant-ungulate ecosystems more feasible. It is likely that these approaches will be increasingly utilized to incorporate the spatial dimension into analyses of plant-herbivore interactions.

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Perspectives and processes in revegetation of arid and semiarid rangelands

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Abstract

Range revegetation research has been dominated by empirical studies that provide some information about what works or does not work under a given set of conditions, but tell us little or nothing about the underlying ecological processes. Research has emphasized the establishment of vigorous exotic grasses on specific sites rather than the establishment of persistent, biologically diverse plant communities. A more mechanistic research approach is needed to better understand factors governing germination, seedling establishment, and plant community development in natural and synthetic systems to guide revegetation toward biological diversity. This paper evaluates selected aspects of the present knowledge of revegetation science on arid and semiarid lands, and attempts to identify areas for future research direction. Specific concepts and aspects of succession and plant community development, such as seedbed ecology, temporal and spatial patterns of resource availability and use, species life history traits, and species interactions are important areas of research. Continuous measurement of detailed environmental and biological data at the appropriate scale (down to the size of small seeds) will allow development of mechanistic models which can be used to predict plant establishment and community development for different environmental conditions.

Key Words: seedbed ecology, succession, simulation modeling, competition, vegetation structure

Rangeland revegetation emerged as an applied science in the U.S. about 100 years ago, following a noticeable downward trend in range condition associated with the settlement and intensive use of arid and semiarid lands. From the early 1890's to the mid 1930's, revegetation efforts attempted to halt land degradation resulting from past stocking practices with domestic animals and the abandonment of cultivated former rangeland. Early revegetation efforts relied heavily upon conventional agricultural principles and practices, and were largely unsuccessful because seed was only available for cultivated forage plants adapted to more mesic environments and site preparation methods were often inadequate (Stoddart et al. 1975). Since the mid 1930's, development of improved plant materials, equipment, and site preparation and planting methods have allowed great progress in the revegetation and improvement of deteriorated grazing land, cropland, recreational land, and wildlife habitat. Revegetation technology for more drastic disturbances, such as those associated with energy and mineral extraction, developed markedly during the 1960's and 1970's with the passage of state and federal legislation affecting land reclamation (DePuit 1986).

Revegetation of arid and semiarid rangelands where annual precipitation is less than 600 mm is constrained, variably influenced, and complicated by the nature of land disturbances and widely divergent climatic and site conditions (DePuit 1986). The size, intensity, frequency, and regularity of occurrence of disturbances vary considerably, and play a major role in community

development and organization (Bazzaz 1983). Climatic factors, primarily low and erratic precipitation and extremes in temperature, exert an overriding effect on the success or failure of a revegetation practice, regardless of the intensity of manipulation treatments used to prepare seedbeds and control undesirable plants (Bleak et al. 1965, Robocker et al. 1965, and Tadmor et al. 1968). Opportunities for establishing a stand by natural or artificial revegetation arise at unpredictable intervals over time. Silcock (1986) estimated that favorable establishment conditions would occur 1 year out of 4 in semiarid regions of Australia. Bleak et al. (1965) suggested that limited precipitation on arid salt desert shrublands in the Great Basin may only allow natural or artificially induced seedling recruitment once or twice every 15 years.

Revegetation has developed more as a technology than as a science over the past several decades. Most research efforts have been site-specific, short-term, empirical studies focused on the immediate problems of plant establishment and soil stability rather than long-term, basic studies focused on the processes of plant establishment and community development (Cairns 1987, DePuit 1989). Extensive testing of different species and site preparation and planting techniques on a variety of sites over many years has emphasized the establishment of exotic perennial grasses in monocultures or simple synthetic communities, but has not provided the guidelines for establishing persistent, biologically diverse plant communities for meeting currently emphasized multiple-use goals. We need a more mechanistic approach in revegetation research to identify and characterize factors influencing the development and persistence of plant communities so that we can determine the potential and the methodologies for establishing biologically diverse communities.

Our purpose in this paper is to provide perspectives on selected aspects of the present state of knowledge of revegetation science in arid and semiarid regions, and identify areas for future research direction. We discuss: (1) the processes of succession because they provide the conceptual basis for planning and evaluating rangeland revegetation projects; (2) vegetation structure because of increasing emphasis being placed on biological diversity and multiple use of rangelands; and (3) seedbed ecology because seed germination and seedling establishment are the most vulnerable stages in the development of natural and synthetic plant communities in arid and semiarid regions. This discussion draws heavily from the emerging science of restoration ecology which focuses on how to reconstruct functional ecosystems on drastically disturbed lands.

Succession/Vegetation Structuring

Natural revegetation tends to be slow and stochastic on arid and semiarid rangelands, where water frequently limits or prevents plant establishment and growth. In contrast, artificial revegetation approaches attempt to compress the process of plant establishment into a single period, regardless of our inability to predict environmental episodes necessary to drive germination and seedling establishment. As a result, many land managers conceptualize revegetation of disturbed rangelands as an instantaneous phenomenon, where plants are introduced and rapidly establish to form a permanent, static community (DePuit 1986). This perception is

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Manuscript accepted 4 May 1991.

invalid on many rangelands, where natural or synthetic community development is a long-term, dynamic process that is influenced by factors of disturbance, microsite heterogeneity, climatic fluctuation, and life history attributes of plant species.

The concepts of succession provide the theoretical basis for revegetation. The processes of succession determine the rate and nature of initial revegetation, and continue to influence plant community development long after treatments have been implemented (Redente and DePuit 1988). MacMahon (1987) and Redente and DePuit (1988) have given a modern interpretation to Clementsian (Clements 1916, 1928) processes of succession (i.e., migration, ecesis (establishment), competition, reaction, and stabilization) to try to better understand how succession can be manipulated through reclamation practices on drastically disturbed lands. They concluded that we presently best understand and can most effectively modify the initial processes of succession (i.e., migration and ecesis). Practices like topsoiling, preparing seedbeds, applying fertilizers and amendments, and seeding and transplanting alter the migration of propagules and enhance plant establishment. However, our understanding of the subsequent processes of competition, reaction, and stabilization is seriously lacking. A better understanding of the relationships among plants, animals, microorganisms, soil processes, and climatic factors is needed in order to reestablish stable, functional communities on disturbed rangelands (MacMahon 1987, M.F. Allen 1988, El-Tayeb 1989).

Clements (1916, 1928) displayed considerable insight when he developed the previously mentioned processes of succession. However, he oversimplified the overall phenomenon of succession with his concepts of single equilibrium communities and deterministic successional pathways. These concepts were formulated into a successional approach that is still used as the basis for developing and evaluating revegetation. While these concepts may be applicable in subhumid prairie communities studied by Clements and others, they may not be suited to plant communities in arid and semiarid regions where vegetation establishment and change are often responses to exceptional events rather than average conditions (Westoby 1980). Westoby et al. (1989) recently summarized how current ecological (successional) theory allows for alternative stable states, discontinuous and irreversible transitions, nonequilibrium communities, and stochastic effects in succession. They proposed that in many rangeland situations, community dynamics can be more accurately described as a set of discrete states of vegetation and a set of discrete transitions between states, rather than as steady vegetation change along a single continuum. The transitions between the various states are triggered by natural events (weather, fire), by management practices (revegetation, prescribed burning, change in stocking rate), or a combination of the two. Once the states and transitions are known for an area, a land manager could determine under what circumstances revegetation practices would provide a favorable transition or an unfavorable transition.

Discontinuous transitions and alternative stable states have been observed on drastically disturbed rangelands where the major revegetation goal, in many instances, is to manipulate succession toward a replica of a pre-disturbance plant community. E.B. Allen (1988) developed conceptual models for reconstructed sagebrush (*Artemisia*)-grassland communities in Wyoming to illustrate that different rates and patterns of natural succession could eventually result in a pre-disturbance vegetation, whereas a different trajectory of succession would result in a community with a different species composition. Different trajectories could be caused by chronic edaphic changes, the introduction of persistent alien species, and the absence of essential symbiotic microbes. Many past revegetation efforts on disturbed rangelands have influenced the trajectory of succession. Monocultures of crested wheatgrass

[*Agropyron desertorum* (Fisch. ex Link) Schult.] in the Great Basin and Lehmann lovegrass (*Eragrostis lehmanniana* Nees) in the Southwest have remained fairly stable and have resisted the invasion of many native grasses and shrubs for decades (Hull and Klomp 1966, Bock et al. 1986).

Concerns about biological diversity and multiple use have directed attention away from the establishment of monocultures to that of more complex synthetic communities that are representative of natural communities. Although the ecological advantages and resource benefits of mixed communities have been frequently noted (Keller 1979, Brown and Hallman 1984, Valentine 1989), attempts to establish mixed communities have often been unsuccessful due to differential adaptability, response to herbivory, and competitiveness of the seeded species, which, after all, were chosen for their vigor (Harris and Dobrowolski 1986, Roundy and Call 1988). The highly competitive nature of many herbaceous and woody species has been blamed for the failure of many perennial grass revegetation attempts on arid and semiarid rangelands (Roundy and Call 1988). Much of the effort in manipulation of range vegetation has been directed at the control of competitive woody species to enhance natural or artificial revegetation of perennial herbaceous species. The resultant plant communities may or may not be more diverse than the previous, woody-dominated communities, which are themselves often lacking in diversity due to the loss of native herbaceous species. Revegetation science in the future must deal with the feasibility and specifics of establishing compatible species to create diversity.

Although Clements (1916) emphasized the importance of competition in species interactions (as have many range ecologists), other interactions including various mutualisms and predator-prey relations (MacMahon 1987) may facilitate vegetation development (Connell and Slatyer 1977). The effects of shrubs on the environment that benefit establishment and production of associated plants are a good example of these interactions (West 1989). Although shrubs and clusters of shrubs may be allelopathic and/or detrimentally competitive with and reduce productivity of herbaceous vegetation in many cases, they may moderate some stressful environments and increase community productivity in other cases. Shrubs may positively affect water availability. They intercept water from light rains and snow. They may increase infiltration rate and waterholding capacity by improving soil structure through reducing raindrop impact and adding organic matter from litterfall, as well as providing habitat for burrowing animals which create macropores. These processes may even result in more favorable soil morphology for plant growth (such as a greater depth to restrictive horizons) under some shrubs.

Shrubs may also be associated with favorable soil fertility and seedbanks for plant establishment. Shrubs catch wind-blown soil, seeds, and mycorrhizal spores, provide resting sites for animals to bring in nutrients and seeds, and concentrate nutrients through absorption and fixation by roots. Shrub canopies reduce irradiance and reradiation and affect understory temperatures, which may reduce evapotranspiration and increase nutrient cycling. Shrubs may even help reduce insect herbivory of associated plants by providing habitat for spiders and other predators.

These observations, summarized from West (1989), indicate that many important ecological processes are associated with the horizontal and vertical structure of plant communities. These important considerations have often been ignored in revegetation. In some cases, appropriate overstory plantings may increase establishment of understory species, such as do natural nurse plants (Wood and del Moral 1986, Franco and Nobel 1988). The presence of shrubs or trees may also significantly increase the productivity of associated grasses compared to that in shrub-free grass stands (Rumbaugh et al. 1982, Frost and McDougald 1989). An impor-

tant challenge for revegetation and ecological restoration science is to determine the requirements and positive characteristics of different species, and the planting patterns which maximize ecological productivity and stability (Aber 1987).

It is important that we have the capability to establish complex communities; however, their complexity may obscure our understanding of processes critical in their assembly and development. We could better understand community development, as agriculturalists and foresters do, by assembling and disassembling simplified communities that are similar in critical ways to more complex communities (Jordan et al. 1987). By reproducing the essentials, in terms of growth forms, spatial patterns, and interactions, critical factors such as community structure and function can be understood more clearly. This understanding of the processes that affect a few key species in a simple synthetic community can be extended to the more complex community and possibly to other communities (Gilpin 1987).

Besides the need for a better understanding of the effects of specific plants on their environment and their neighbors, there is also a need for understanding community-wide processes. Research could be directed toward determining the productivity of assemblies of species with known beneficial characteristics, such as nitrogen fixation, mycorrhizal potential, and potential root and canopy structure compatibility.

Range revegetation by Nechoeva (1985) and colleagues in Soviet Central Asia is an example of an attempt to structure ecologically stable mixed shrub-herbaceous communities. The resource goal was to establish communities to fulfill the seasonal dietary requirements for sheep. Shrub species were selected for known environmental tolerances and expected compatibility to more fully utilize soil water and nutrient resources and radiant energy. Competitive ability, phenology, potential allelopathy, habit-forming ability (or the potential modification of the environment) as well as root distribution were considered in species selection. Shrubs were seeded in various species combinations in strips plowed through sedge and grass-dominated rangeland. The plowed strips, or "couisses", accumulated soil water in the winter which allowed shrubs to germinate. Over time, grasses and sedges filled back in under the shrubs and shrub species density equilibrated. Creation of these "agrophytocenes" increased forage production by up to 8 times, provided a more nutritional year-round diet for sheep, and maintained greater production during drought than native rangeland. The potential for structuring useful and productive "agrophytocenes" is probably quite high, but will require considerable research effort and a better basic understanding of the characteristics of numerous species.

Seedbed Ecology

Plant establishment by seedling recruitment, the dominant type of regeneration for most species in rangeland communities, is only successful when plant requirements for seed germination, seedling establishment, and subsequent growth are matched with the microenvironmental factors of the seedbed (Grubb 1977, Harper 1977). Revegetation literature abounds with studies that describe germination and seedling responses under controlled environmental conditions that are not representative of stochastic environmental conditions found in the field. Conversely, field studies describe germination and seedling responses under natural conditions, but in most cases, critical environmental factors have not been measured in adequate detail to accurately assess how seeds and seedlings are "sensing" and responding to their microenvironment (Mayer 1986). Despite such shortcomings, these studies have improved our knowledge of seedbed environments and their influence on germination and seedling establishment. In fact, comparisons of germination and seedling development characteristics

among species in a community offer some clues about how species partition the habitat and develop the structure of a community (Burton et al. 1988, and Evans and Young 1987).

We still try to compensate for our lack of understanding of plant-site relationships by increasing the number of species in seeding mixtures and/or increasing seeding rates (Vallentine 1989). However, seedling recruitment during natural and artificial revegetation is a result of the number of seeds in favorable microsites, or "safe sites", in the seedbed rather than the total number of available seeds (Harper et al. 1965, Young 1988). This number is a function of seed and seedbed characteristics. Seeds of most species germinate best when buried at a proper depth in a firm seedbed. Much of revegetation technology has dealt with the development and application of seedbed preparation and sowing methods to place seeds at the proper depth and in favorable microsites. Although seed burial recommendations have been made for different-sized seeds (Vallentine 1989), few studies have been undertaken to determine where different sowing methods actually place seeds in the seedbed and from which depths or locations seedlings successfully emerge. Using high seeding rates and an intensive sampling procedure (Winkel and Roundy 1991), Winkel et al. (1991a) determined percentages of seeds buried and depth of emergence of seedlings in relation to seedbed treatments. The percentage of seeds buried above the maximum depth of emergence, or biological limit, could then be calculated. The percentage of seeds on the surface, within and below the depth interval of emergence, varied with seed size, seedbed preparation treatment, and rainfall conditions. These kinds of data are needed to better define safe sites and determine the effectiveness of seedbed preparation methods.

Many small-seeded species and certain species with specific physiological requirements (i.e., light for phytochrome transformation, fluctuating temperatures, lack of seed reserves for emergence) must be located on the seedbed surface for germination to occur (Mayer 1986, Young et al. 1987). The role of seed appendages in facilitating seedling establishment of seeds on the soil surface has been recognized (Booth 1987) but has not generally been considered or exploited in revegetation technology. Site conditions (i.e., topography, rockiness, and type and extent of disturbance) and costs can restrict conventional methods of tilling and seeding on many rangelands. A better understanding of surface soil safe site characteristics and functional seed morphology is needed to determine appropriate species, sites, and management to permit less expensive, less capital-intensive seeding methods. These may include broadcast seeding certain seeds with appropriate appendages, size, or morphology on natural seedbeds without soil coverage. Also included might be the use of animals (Simao Neto et al. 1987) or natural drainages (J.R. Barrow, personal communication) for dispersal of seeds and enhancement of seedling establishment.

Favorable water and temperature conditions for germination and establishment on or near the surface are associated with surface soil microtopographical features such as cracks, depressions, rocks/gravel, and plant litter, and proximity to neighboring vegetation (Harper et al. 1965, Harper 1977). Only a few detailed studies (Evans and Young 1987, Fowler 1988, Winkel et al. 1991b) have determined the types of microsites that are adequate for germination and establishment of a limited number of range species. Surface cracks, depressions, and/or obstructions have been shown to modify temperature and moisture conditions in a variety of environments. In a classic study, Harper et al. (1965) reported increased emergence from seeds of *Plantago* spp. placed in depressions (1.25–2.50-cm deep) and near ridges (1.25–2.50-cm above the surface) in an artificial seedbed. They also reported increased emergence of *Bromus rigidus* Roth when seeds were sown on

seedbeds comprised of small aggregates (<1.25-cm diameter), and of *B. madritensis* L. when seeds were sown on seedbeds comprised of larger aggregates (3–5-cm diameter). Differences in emergence of the *Bromus* species were related to the types of contact different shaped seeds made with the water-supplying surface of the aggregates. Fowler (1988) observed that rocks (no mention of size) created safe microsites for red threeawn (*Aristida longiseta* Steud.) and Texas grama (*Bouteloua rigidiseta* (Steud.) Hitchc.) in a shortgrass community in Texas by providing shade and reducing evaporative losses. In a controlled environment study, Winkel et al. (1991b) determined the effects of several natural microsites, typical of semidesert grasslands in the southwestern U.S., on seedling emergence of 3 warm-season perennial grasses in relation to soil water conditions. Under all soil water conditions, emergence of sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), blue panic (*Panicum antidotale* Retz.), and Cochise lovegrass (*Eragrostis lehmanniana* Nees × *E. tricophera* (Nutt.) Wood) from surface-sown seed was highest from gravel (2–5-mm diameter, 10-mm deep), followed by cracks (2–5-mm wide, 15–20-mm deep, and 80–100-mm long), and least from the bare soil surface. Soil water potential remained above -1.5 MPa several days longer in the gravel microsites than on the bare surface sites as water became more limiting, indicating that seedlings in gravel sites may not be subject to desiccation before the next rainfall event.

Seedbed ecology studies in sagebrush-grassland communities in the Great Basin region demonstrated that more seedlings of Wyoming big sagebrush (*Artemisia tridentata* Nutt. spp. *wyomingensis* Beetle and Young), Thurberry needlegrass (*Stipa thurberiana* Piper), downy brome (*Bromus tectorum* L.), and medusahead [*Taeniatherum asperum* (Sim.) Nevski] emerged from cracks and pits than on the bare soil surface (Eckert et al. 1986, Evans and Young 1987). Microenvironmental monitoring indicated that depressed sites retained moisture at the surface longer and had more favorable atmospheric and temperature regimes than the smooth soil surface. Depressions also created more favorable conditions for soil coverage of seeds (i.e., trapping wind-blown particles, sloughing of sides of depressions). Development of the deep-furrow rangeland drill and the rangeland imprinter was based, in part, on this safe-site concept, and this equipment has enhanced seeding success on some arid and semiarid soils (Asher and Eckert 1973, Haferkamp et al. 1987).

The type and amount of litter on the soil surface can have variable effects on seedbed microenvironments and seedling recruitment. In southwestern U.S. semidesert grasslands, Winkel et al. (1991b) found emergence of 3 warm-season perennial grasses was greater when surface sown seed was covered with litter (excelsior cut into 20–50-mm lengths, 10–20-mm deep) than not; however, emergence was lower than from a gravel-covered soil surface. Evans and Young (1987) reported much greater emergence of downy brome, medusahead, and Russian thistle (*Salsola iberica* Sennen & Paul) from seeds under litter than from seeds on the soil surface in an annual rangeland community in Nevada. Litter greatly modified diurnal and seasonal patterns of air temperature and diurnal range of relative humidity at the soil surface, and delayed soil water depletion in the soil surface layer. The atrazine-fallow method for control of downy brome and subsequent establishment of perennial grasses was based on the concept of reducing litter accumulations on the soil surface to decrease downy brome seedling establishment (Eckert and Evans 1967).

In contrast to the species-litter responses above, Evans and Young (1987) noted that tumble mustard (*Sisymbrium altissimum* L.) had greater germination and seedling establishment on a bare soil surface than under litter. The seedcoat of this species produces a mucilage upon wetting that gradually dries, conserving moisture and providing more continuous contact between the seed and the

soil particles in the seedbed. In a shortgrass community in Texas, Fowler (1988) observed that establishment of red threeawn and Texas grama was greater on microsites free or almost free of litter. In this more mesic environment, even small amounts of litter may harbor pathogens that reduce germination and seedling survival when soil moisture and soil surface relative humidity increase following rainfall.

The type and depth of litter has also been noted to influence the establishment of shrub and grass seedlings in sagebrush-grassland and salt desert shrub communities in the Great Basin. The accumulation of leaves of basin big sagebrush (*Artemisia tridentata* Nutt. spp. *tridentata*) under shrub canopies may prevent seeds from reaching the soil surface whereas herbaceous litter creates a porous media that allows seeds to contact the soil surface (Young 1988). Soil mounds beneath shrubs have a higher organic matter content and are more granular in structure than soils in nearby vegetation-free interspaces that form vesicular crusts which restrict water infiltration and seedling emergence. Eckert et al. (1978) studied the influence of soil morphological characteristics of these surfaces and found that perennial grass establishment following shrub removal and drill seeding was much greater on shrub mounds, where litter had mineralized, than in interspaces.

The proximity and developmental stage of neighboring plants can also influence the suitability of a seedbed microsite. In the shrub mound—bare interspace pattern in the Great Basin, the establishment of shrub and herbaceous species is further complicated by competitive interactions with established shrubs. The most favorable site for establishment based on soil surface conditions is near the margin of the shrub canopy, but most developing seedlings cannot effectively compete for soil water in such close proximity with established shrubs (Young 1988). In most instances, seedlings establish in cracks in the shrub interspaces until shrubs naturally senesce or are eliminated by a disturbance. In contrast to the observations of Young (1988), Owens and Norton (1989) reported greater survival for basin big sagebrush sheltered by mature sagebrush than for unsheltered seedlings in central Utah. They suggested that higher survival may have been partially due to protection from desiccation. In the Patagonian arid steppe of Argentina, seedling survival of *Bromus setifolius* Presl. was much greater in bare interspace microsites than in microsites adjacent to shrubs (*Mulinum spinosum* (Cav.) Pers.) encircled by a ring of bunchgrasses (Soriano and Sala 1986). There was no difference in germination between the 2 microsites; but, as soil water became more limiting during the summer period, soil in bare interspaces dried out at a slower rate. Soriano and Sala (1986) suggested that to accelerate community recovery, there must be an increase in the number of seeds at optimum microsites or an increase in the density of these microsites.

In a patchy shortgrass community in Texas, Fowler (1988) noted that safe microsites for the establishment of red threeawn and Texas grama were not necessarily characterized by a reduced density of surrounding plants. Both species survived better and grew larger the first year if they were located within 2 cm of seedlings or juvenile plants of either species. Effects of improved soil water and atmospheric temperature conditions apparently outweighed the effects of competition between seedlings and juvenile plants in this dry environment. A direct positive effect of neighbors on seedlings (i.e., facilitation) was unlikely; rather, the presence or a surviving neighbor was an indication that the microsite had been favorable for the neighboring plant in the past, and could still be favorable for further recruitment. However, Fowler (1988) also observed that the safeness of microsites within a quadrat (45 × 90 cm) varied from year to year and even month to month, thus preventing these 2 grass species from ever developing stable spatial age and size distributions within a site.

To better understand recruitment and subsequent growth in naturally and artificially revegetated communities, one can use niche quantification and site-matching techniques to select plant species that would improve long-term community stability (Burton et al. 1988). Variability in soil moisture and other attributes can be described by a frequency distribution of soil measurements made over time or over space in experimental growth studies or by direct gradient analysis in the field (Fig. 1). The frequency distribution

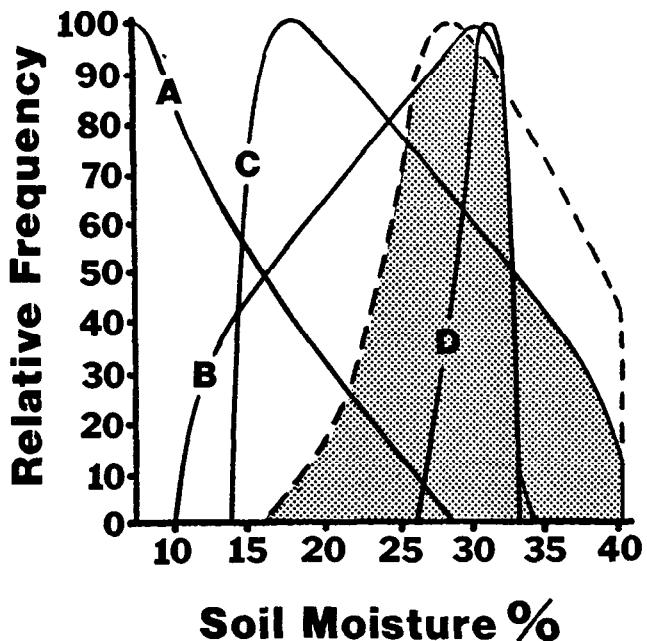


Fig. 1. Overlay of standardized moisture response curves for 4 species (lines A through D) and a moisture-defined environmental space (dashed line) for a hypothetical range site. The shaded area represents the maximum occupancy (83% in this example) of the environmental space possible for this set of species. Note the overlap between species, particularly species B and D, along the soil moisture gradient. Adapted from Burton et al. 1988.

can be smoothed to form a curve and the area under the curve is defined as the available environmental space for that resource. Environmental space approximates the range and frequency of conditions to which the plants will be exposed. Gradient response curves, describing the realized niche of each species can then be overlaid on the environmental space curve (Fig. 1). Niche overlap can be estimated, and the best mixture of species can be selected to match the site, filling the environmental space as fully as possible to prevent invasion by undesirable species.

Predicting Germination/Seedling Responses

We need to better recognize that revegetation processes in rangeland communities, particularly in arid and semiarid regions, are regulated by episodic rather than average environmental conditions. Successful establishment of a species may require the co-occurrence of a seed source, seed placement in favorable microsites, precipitation adequate to stimulate germination, recurrent precipitation for seedling establishment, and possibly low herbivory and/or absence of competition during establishment (Noble 1986). According to the state-and-transition model of Westoby et al. (1989), emphasis could be placed on estimating the probabilities of climatic conditions relevant to revegetation processes and implementing revegetation practices where and when conducive climatic conditions are likely.

To really understand the processes and effectiveness of different methods used to enhance seedling establishment, we need to mea-

sure the seed microenvironment and corresponding biological responses (germination, root growth) associated with these methods. We need to measure natural as well as modified seedbeds to determine the importance of factors such as litter, gravel, microtopography and salts (for natural osmoconditioning-Roundy 1987) in creating suitable temperature and moisture pretreatments and establishment conditions for different precipitation scenarios. Unfortunately, it is not practical to characterize seed environments for a wide variety of range sites and microsites. An alternative approach involves the modeling of appropriate water and temperature conditions for germination and seedling development in seedbeds based on climatic data. This would allow one to predict the effects of weather and revegetation treatments on seedbed conditions, and indicate what biological responses are important to establishment under different conditions.

Several models have been developed to estimate soil temperature and water for agricultural and rangeland soils, but these models have not been adequately tested for simulation of soil temperature and water in the surface layer of the seedbed (Wight and Hanson 1987). The major problem in developing and testing models for simulating soil water and temperature dynamics in the surface layer is the lack of appropriate, continuously monitored field data.

Spatial and temporal variability in soil temperature in the surface layer is easily measured by thermistors or thermocouples but the measurement of surface soil water content and/or water potential at the microscale of most seeds and seedlings is more difficult because of sampling techniques and sensor characteristics (Harper et al. 1965). Winkel et al. (1991b) determined the gravimetric soil water content from the top 5 mm of mineral soil from gravel, litter, and bare microsites and still had difficulty differentiating why Cochise lovegrass seedlings had greater emergence from gravel than litter. Although soil water content under litter was similar to or higher than under gravel, they speculated that soil water and relative humidity in the immediate vicinity of seeds may have been greater under gravel than litter. Unfortunately, they could not measure these parameters at the appropriate scale of the small lovegrass seeds. In the previously described surface microtopography-soil water study of Evans and Young (1972), the researchers were forced to make pits 3 by 6 cm and 3, 6, or 9-cm deep (larger than naturally occurring depressions) because of the size of gypsum resistance blocks used to measure soil matric potential. In addition, gypsum blocks are only sensitive from -0.5 to -1.5 MPa, preventing the measurement of the full range of diurnal and seasonal moisture conditions in the surface layer in dry environments (Kramer 1983). Fiberglass-resistance-type soil cells are slightly smaller in size and measure a wider range of soil matric potentials (near-saturation to near-air dry) than gypsum blocks (Reynolds et al. 1987), and thus may be more appropriate in the surface layer. However, the fiberglass soil cells still do not measure soil matric potential at the microscale required to sense the immediate environment of a seed. Psychrometers measure total soil water potential for a very small fraction of the soil volume, but they are sensitive to temperature gradients, and thus give inaccurate readings near the soil surface (Brown and Bartos 1982). The neutron scattering technique samples a sphere of soil with a radius of 10–30 cm making it difficult to accurately measure soil water content in the surface layer (Rundel and Jarrell 1989). A relatively new technique, time-domain reflectrometry (TDR), shows promise for measuring soil water content in rangeland soils; however, as with neutron scattering, TDR samples a large volume of soil, making it less sensitive to microscale variations in the seedbed (Rundel and Jarrell 1989). Thus, the development of sensors that can accurately measure surface soil moisture content at a fine scale on a continuous basis is needed to provide more meaningful soil moisture data

for seedbed models.

As we refine our measurement and modeling techniques, we can better predict the effects of weather and revegetation treatments on seedbed conditions, and indicate what biological responses are important to establishment under different conditions. The development of accurate models would also permit the linking of laboratory-measured germination and seedling responses to different field conditions (Wight and Hanson 1987).

Conclusions

Over the past several decades, revegetation technology has progressed more rapidly than revegetation science. Extensive empirical species trials on different sites have provided techniques and guidelines mainly for successfully establishing a few vigorous exotic grasses. To establish more diverse plant communities we need to better understand the successional processes associated with plant establishment and community development. To do so will require the detailed study of the biological requirements and resource use of different species in relation to environmental conditions. By measuring and modeling the physical environment in relation to biological responses we should be able to better determine the quantitative effects of different factors on the successful establishment and persistence of more functional synthetic plant communities.

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Plant-plant interactions affecting plant establishment and persistence on revegetated rangeland

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Abstract

Restoration and revegetation of rangeland ecosystems is based on knowledge of abiotic and biotic interactions that affect plant establishment. Once plants become autotrophic, interactions within and between plant species may occur and these interactions may range from antagonistic to mutualistic. This full range of potential interactions needs to be considered to ensure successful revegetation. At the intraspecific level, we propose the development and use of density-yield diagrams for rangeland species. These diagrams would be based on the self-thinning principle, that aboveground biomass is related to plant density and to the dynamic process of density-dependent mortality. The proposed approach would be used to determine optimum seeding rates, and to predict future biomass of revegetated rangeland. At the interspecific level, competitive relationships of species used to reseed rangelands need to be identified to enhance the probability that species will coexist and thereby facilitate greater species diversity on the site. A diversity of species and growth forms may provide a more stable cover and productivity than a monoculture on sites characterized by environmental variability while potentially enhancing nutrient status for the site.

Key Words: competition, mutualism, resource partitioning, revegetation, self-thinning, species mixtures, stress tolerance

Revegetation may range from a total restoration of the original ecosystem, to rehabilitation (partial restoration), to natural reseeding, to a replacement of the original ecosystem with an alternative ecosystem (Bradshaw 1984). Regardless of the form of revegetation, our expectation of its outcome should be based on our knowledge of abiotic and biotic interactions that affect plant establishment. Unfortunately, our understanding of mechanisms regulating ecosystem processes is often limited. As a result, the applicability of several ecological paradigms has been rightfully questioned. For example, there is considerable debate as to what forces drive succession (Connell and Slatyer 1977, MacMahon 1981, Westoby et al. 1989) and as to the importance of competition in determining community composition (Schoener 1983, Connell 1983). No longer is the competitive exclusion principle (Gause 1934, Hardin 1960) accepted as the best explanation of species diversity and coexistence (Silvertown 1987). An array of alternative hypotheses have been proposed to explain spatial and temporal relationships of species in communities. These include the regeneration niche hypothesis (Grubb 1977), the resource ratio hypothesis (Tilman 1982), the aggregation hypothesis (Shmida and Ellner 1984), the gap-phase replacement hypothesis (Pickett and White 1985) and the storage effect hypothesis (Warner and Chesson 1985).

An understanding of biotic interactions and successional pro-

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Authors wish to thank A.L. Aradottir, N. Fowler, T.E. Fulbright, D.N. Ueckert, and S. Zitzer for critical review of earlier drafts of the manuscript; and C. Call and B. Roundy for organizing the symposium that brought about our collaboration. Two anonymous reviewers made helpful suggestions which improved the final draft. This paper was partially funded by NSF grant BSR 87-05492, Utah Mineral Lease Funds NR-1181, and Utah Agricultural Experiment Station Project 641 and 891 to DAP and by USDA grants 89-38300-4508 and 89-38300-3625 and Texas Agricultural Experiment Station Project 6717 to SA.

Manuscript accepted 6 May 1991.

cesses is central to revegetation, since strategies for rehabilitation and restoration typically center around augmenting, enhancing, or accelerating changes in species composition. The key to restoring native plant communities, in many cases, lies with identifying and overcoming factors that impede or restrict ecosystem development (Bradshaw 1987). Although descriptions of species composition through time provide valuable information regarding community change, they seldom provide insight as to why changes occurred. We must examine adaptations and processes that confer persistence and compatibility or incompatibility to understand why some species coexist while others do not.

Our purpose in this review is to focus on biotic interactions that are related to repairing rangeland ecosystems by revegetation. This is not an exhaustive review, but rather a synopsis of how plant-plant interactions determine success or failure of rangeland revegetation efforts. We recognize that animals also play a major role in the success of revegetation and we address their impacts in a companion paper (Archer and Pyke 1991). Throughout this paper, we relate the impact of these interactions to succession and landscape ecology and we suggest future research directions that will fill gaps in our current knowledge of rangeland revegetation and restoration.

Intraspecific Associations

Size, Biomass, and Density Relationships

Once plants become autotrophic, they begin to interact with both conspecific individuals and with plants of other species growing in the immediate vicinity. These interactions vary from being antagonistic (e.g., competitive) to being mutualistic (e.g., mycorrhizae-plant associations). A knowledge of mechanisms of plant interactions is required to transform range revegetation from a correlative science to a predictive science.

Ecological theory relating density-dependent plant interactions has been largely unexplored in rangeland revegetation research. The self-thinning principle, that aboveground plant biomass is related to initial plant density and to the dynamic process of density-dependent mortality over time, has been widely accepted in forest management (Drew and Flewelling 1977) and in plant ecology (White 1981, Westoby 1984). The principle has recently come under some scrutiny in plant ecology (Weller 1987) and may require carefully designed experiments to validate (Lonsdale 1990), but the original interpretation of the principle as an upper boundary for plant yield appears to remain valid for individual species (Osawa and Sugita 1989). This principle is conspicuously absent from range improvement (Vallentine 1989) and general range management texts (Stoddart et al. 1975, Holechek et al. 1989), although it is recognized in many fields of plant science.

The principle is mathematically stated in 2 forms. One form relates individual plant biomass to density,

$$\log w = \log K - 1.5(\log d), \quad (\text{eq. 1})$$

where w is the mean plant biomass, d is the mean number of plants per unit area and K is a constant. The alternative form relates yield per unit area to density,

$$\log b = \log C - 0.5(\log d),$$

$$(eq. 2)$$

where b is mean aboveground biomass per unit area and C is a constant.

The outcome of these self-thinning relationships in revegetated rangeland is evident in studies that examine the effect of initial seeding rate on plant density (e.g., Hull and Holmgren 1964, Hull and Klomp 1967). However, it is difficult to demonstrate the principle with these studies since they rarely provide density (plants per unit area) and yield per unit area for the first 3 to 5 years after seeding. Foresters not only recognize the importance of self-thinning, but they use this principle to explain forest stand development and to guide management decisions. Drew and Flewelling (1977, 1979) describe 3 lines in a density-volume relationship (proportional to the density-mass relationship) (Fig. 1). Recent studies suggest that the slope of these lines may vary depending on the species (Weller 1987, Lonsdale 1990); however, we have used a slope of -0.5 for each line for explanatory purposes while recognizing that species-specific estimates of slope will need to be determined.

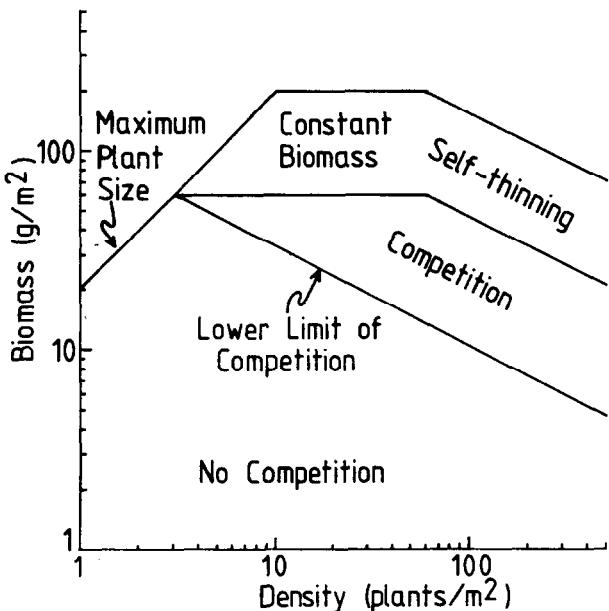


Fig. 1. Relationship between plant density and biomass for a hypothetical plant species (after Drew and Flewelling 1977).

The upper line describes the maximum size a stand of plants can attain at a given density and represents the upper morphological and physiological limit in size for a species grown without interspecific competitors. The next lower line describes the lower limit of the 'zone of imminent competition mortality' or a zone of sizes and densities where density-dependent mortality occurs. This zone is equivalent to the self-thinning band of Westoby (1984). The lowest line approximates the initiation of competition between plants. Between the competition line and the lower limit of density-dependent mortality is a zone of competition without density-dependent mortality. Density-dependent mortality will not occur in this zone although relative growth rates will decrease as resources become increasingly limiting. As a result, actual biomass at time t (b_t) will be less than the biomass which would have accumulated in the absence of competition (B_t) (Fig. 2).

Our hypothetical example also illustrates how the dynamic process of self-thinning and competition may reduce the density of a high-density population (300 plants/m^2) to levels comparable to that of a medium density population (40 plants/m^2) while maintaining production that is greater than or equal to the medium

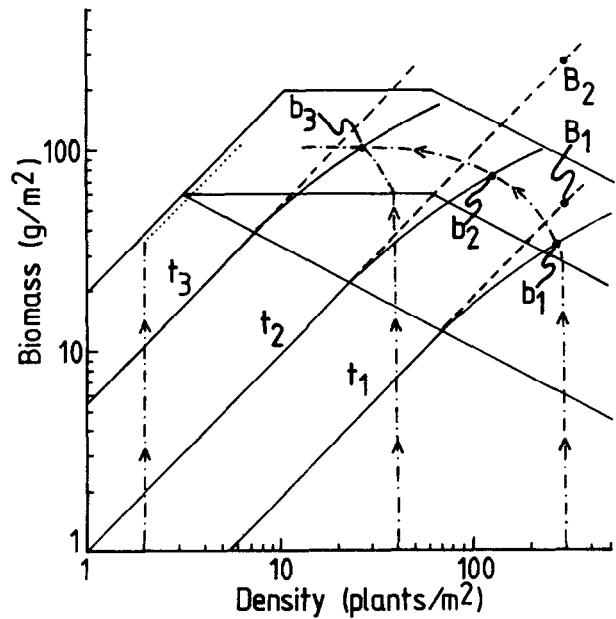


Fig. 2. Biomass of populations (b_t) harvested at times t_1 to t_3 for a range of densities of a hypothetical plant species. In the zones of competition and of density-dependent mortality (see Fig. 1) the dashed line indicates potential biomass (B_t). The dot-dashed lines represent the time trajectories of 3 densities. The dotted line associated with the low density population represents establishment of new individuals.

density population throughout the same time periods (Fig. 2). The high-density population at time t_1 has produced more biomass than the medium density population, but has entered the self-thinning zone. Plant density becomes reduced in this zone as individual survivors continue to increase in size. Both populations by t_3 have similar densities and both are in the zone of constant biomass where production losses resulting from plant mortality are compensated for by increased growth of remaining plants.

There are numerous aspects of revegetation that require experimental examination using this basic principle. If a density-yield diagram similar to Figure 2 was developed for a species, the predictions could be made of the time required to achieve an expected biomass from an initial density of plants. An economic analysis would be required to determine if the increased biomass and density of plants on the high-density site through t_3 was sufficient to warrant the cost of applying nearly 10 times more seed.

Recommended seeding rates are often set as the lowest seeding rate needed to achieve production comparable to that of stands receiving higher seeding rates, but at a rate that allows for density-independent mortality. That rate could be determined as a density slightly higher than the minimum competitive density using Figure 1. This would be the density that could theoretically achieve maximum production with the minimum number of plants. Populations sown at this density would not enter the competitive zone until they had completed density-independent mortality and had achieved their maximum plant size (Fig. 1). Plant densities below this level, for example the low-density population (2 plants/m^2) in Figure 2, would result in yields per unit area that are less than their potential maximum even though the individual plants may achieve their maximum size. Any further increase in yield per unit area would only be achieved through the establishment of new individuals via seedlings or vegetative propagation (dotted line in Figure 2).

There are potential disadvantages of sowing at the minimum density that must be considered in any economic or ecological evaluation: (1) the probability of undesirable plants becoming

established in areas between sown plants will be increased (e.g., McGinnies 1960, Cook et al. 1967, Hull and Klomp 1967); (2) soil stabilization and moisture infiltration may be reduced, while raindrop impact and surface runoff are increased at lower plant densities; (3) larger plants, characteristic of low-density stands, may be more susceptible to grazing than smaller plants characteristic of high-density stands (e.g., Westoby 1980). In addition, the probability of defoliation would be greater and would be spread over fewer individuals in low-density plantings; and (4) relative to high-density stands, low-density stands may produce plants with greater stem-to-leaf ratios making plants less palatable to grazing animals (Cook et al. 1967).

Sowing at densities that will generate early intraspecific competition has advantages and disadvantages. Early intraspecific competition may minimize establishment and seed production of undesirable species. Early competition, however, will also slow the growth of desirable plants and may contribute to mortality if individuals must achieve a minimum size to survive inclement conditions, such as summer drought or winter frost heaving. A tradeoff, therefore, exists between increasing early intraspecific plant density for the purpose of weed control and reducing intra-specific plant density for the purpose of optimizing individual plant size or stand production. Further research is needed to ascertain the optimum density required for maintenance of populations of desired plants while controlling undesirable species.

Interspecific Associations

Competitive Exclusion and Coexistence

Competition for limited resources may determine the presence, absence, or abundance of species in a community and determine their spatial arrangement. The importance of competition has been questioned, particularly for ecosystems with harsh environments (e.g., deserts and tundras). Abiotic stresses rather than competitive interactions may dictate community structure and function in these ecosystems (Grime 1977). Fowler (1986), however, conducted a thorough review of research investigating competition in arid and semiarid plant communities and concluded that competition does occur in these systems, that it involves many different species, and that it is an important determinant of community structure. One or more of the following factors may occur when plants compete for resources: (1) time to reproductive maturity may be increased; (2) growth rates of plants and the frequency and magnitude of viable seed production may be decreased; and (3) susceptibility to density-dependent and density-independent mortality factors may be increased.

These are important factors determining the outcome of revegetation and restoration efforts. In formulating seed mixtures, information on overlap in plant resource requirements and acquisition strategies may help determine: (1) which species are likely to be in direct competition and are therefore inherently incompatible; (2) which species may effectively partition site resources to minimize competitive exclusion and therefore promote coexistence and diversity; and (3) which species may modify site characteristics to facilitate succession and establishment of additional species. It is important to keep in mind in addressing these issues that competition is probably not a continuous, uniform phenomenon in communities. The intensity, frequency, and periodicity of competitive interactions between plants may vary substantially on a seasonal and annual basis in accordance with the stage of life cycle, with patterns of physiological activity, and with resource availability (Connolly et al. 1990). Welden and Slauson (1986) present a theoretical comparison of the importance and the intensity of competition on plant growth.

Diversity and Primary Production

With the recent concern for maintenance of biological diversity,

mixtures of species will likely be used for revegetation to a much greater extent than they have been in the past. Development of community diversity is also potentially important for stability of vegetation cover and productivity. Species in communities have different life-history strategies and adaptations. As a result, their patterns of growth and reproduction vary spatially and temporally and are limited by different combinations of resources or environmental factors. Most research to date has focused on plant responses and adaptations to single features of the environment, but plants in nature often encounter multiple stresses (Chapin et al. 1987). In addition, field experiments frequently indicate that 2 or more resources may simultaneously limit plant growth (Lauenroth et al. 1978, Chapin and Shaver 1985). Fluctuations in weather or resource availability may cause substantial annual variation in productivity of individual species. However, the productivity of the community may be much less variable, since years that are favorable for growth of some species reduce the growth of other species, because of direct plant responses and competitive interactions. Conversely, in stressful years, the productivity of some species may be less affected than that of others (Fig. 3).

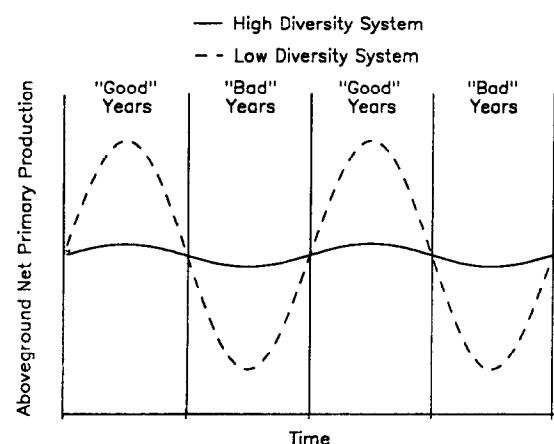


Fig. 3. Hypothetical relationship between species diversity and aboveground net primary production (ANPP) through time. Aboveground net primary production in the low diversity system will be high in years 'good' for species that dominate this system. Conversely, ANPP in the same system will be low in years 'bad' for these species. Fluctuations in productivity in this hypothetical community would therefore be substantial. In contrast, stability of ANPP might be enhanced on sites containing a diverse mixture of species which encompass an array of competitive and stress tolerance strategies. Aboveground net primary production of the high diversity system would not be as high as that of the low diversity system in certain years, but it would not drop as low in other years.

Changes in the relative growth rates and in the abundance of co-occurring species can therefore stabilize ecosystem processes such as primary production, relative to sites with low diversity, and can maximize resource utilization across heterogeneous landscapes over time (McNaughton 1977, Chapin and Shaver 1985, Collins et al. 1987). For example, C₃ plants are typically active early in spring or fall, whereas C₄ plants maintain growth during the warmest, driest portions of the growing season (Williams and Markley 1973, Ode et al. 1980, Sala et al. 1982). In addition, productivity and species composition of landscapes are regulated by edaphic heterogeneity and topography. Species with contrasting photosynthetic physiologies (or other characteristics) may be spatially distributed in accordance with variation in resource availability along gradients within the community (Barnes and Harrison 1982, Barnes et al. 1983, Archer 1984). As a result, a mixture of C₃ and C₄ species may give more stable and sustained annual productivity than a monoculture of either (Heitschmidt et al. 1986).

Stress Tolerance vs. Competitive Ability

Plant attributes pertaining to stress tolerance and competitive ability (Grime 1979) should be considered when formulating seed mixtures. Distinctions between these 2 general categories of plants (Table 1) are based on the idea that there is an evolutionary relationship between intrinsic growth rate and resource availability. Natural selection in sites characterized by favorable environmental conditions and high resource (water, nutrients, light, etc.) availability should favor plants with rapid growth, because these

Table 1. Characteristics of plants selected for competitive ability versus stress tolerance (from Grime 1979, Chapin 1980, Bryant et al. 1983, Gray and Schlesinger 1983).

Competitive plants	Parameter	Stress-tolerant plants
Competition	Primary Selection Pressure	Abiotic Stresses
High	Intrinsic Growth Rate	Low
High	Root and Leaf Turnover	Low
Low	Root:Shoot Ratio	High
Low	Association with Root Symbionts	High
No	Luxury Nutrient Consumption	Yes
High	Allocation Plasticity	Low
High	Susceptibility to Frost, Drought, and Heavy Metals	Low
Large	Belowground Carbon or Nutrient Reserves	Small
High	Capacity to Regenerate Following Defoliation	Low
Low	Integrated Resource Use Efficiency	High
Low	Nutrient Retention in Foliage	High
High	Coupling of Nutrient Release and Uptake	Low

would be most likely to capture resources and to subject slower-growing species to plant-induced stresses associated with shading and depletion of water and nutrients. However, in environmentally harsh sites and in sites where levels of resources are chronically low, conditions suitable for rapid plant growth may occur infrequently. Natural selection under these conditions would favor adaptations conferring tolerance to prevailing forms of abiotic stress and the ability to conserve resources that have been acquired. As a result, the most productive species or cultivars on sites when resources are plentiful may be the least persistent when resources become limiting (e.g., intermediate wheatgrass *Agropyron intermedium* (Host) Beauv.) is productive on mesic sites, but is susceptible to drought, whereas bulbous bluegrass (*Poa bulbosa* L.) is tolerant of drought, but has low yield potential (Valentine 1989). Some species, however, combine favorable aspects of both categories, such as crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) (Shultz.), being tolerant of resource limitations while at the same time being highly competitive in semiarid regions.

Considerations for Formulating Seed Mixtures

Most-seed mixture research on rangelands has taken a 'shotgun' approach; mix several species together and observe their establishment. Establishment and production of seed mixtures of native plants have been compared with that of introduced species in some instances (Doerr et al. 1983, Redente et al. 1984); however, the criteria for formulating multispecies mixtures is typically based on plant-soil and plant-climate relationships. Consideration of competitive relationships and of compatibility among plants in mixture and among desirable and undesirable species is rare.

Species sown in mixtures should be chosen based on sound ecological evidence that they can coexist. Unfortunately, research that provides this evidence is lacking and is needed in the future. Successful coexistence in many cases will depend on morphological or physiological attributes that enable various species at key stages in their life cycle to partition site resources effectively in space (vertical and horizontal, above- and belowground) and in time (seasonal or phenological). In other cases, coexistence can occur when a species exploits a resource more effectively when the resource is rare, while another enjoys the advantage when the resource is abundant (Armstrong and McGehee 1980). Oscillations in resource and species abundance may occur in these instances. Pattern and scale of spatial variability in resource abundance will also affect assessments of compatibility of potential competitors. If there is sufficient heterogeneity in resource abundance, species that would be competitors in more homogeneous environments may coexist via small-scale spatial segregation (Tilman 1980, 1982).

Seed mixtures that contain species with distinctly superior competitive and/or establishment abilities often produce stands with species abundances different from what would be predicted from the proportions of seed sown of each species (DePuit and Coenenberg 1979, Schuman et al. 1982, Redente et al. 1984). Increasing resource availability through fertilizer application or irrigation typically increases yield (Holechek et al. 1981), but may also reduce species diversity (DePuit et al. 1982, Stark and Redente 1985, Biondini and Redente 1986). This inverse relationship between production and diversity, known as the paradox of enrichment (Rosenzweig 1987), results because the competitive dominants are often better able to capitalize on increased resource availability and can therefore increase their biomass or density at the expense of other species (Huston 1979).

Assessing Competition

The competitive balance between species is influenced by the density and the proportion of the competing species. The experimental design most used for evaluating plant mixtures is that of the replacement series (de Wit 1960); however, this approach has recently come under considerable criticism (Mead 1979, Inouye and Schaffer 1981, Jolliffe et al. 1984, Firbank and Watkinson 1985, Connolly 1986, Taylor and Aarssen 1989). In additive-replacement series experiments, with their associated techniques of numerical analysis (Law and Watkinson 1987, Connolly 1987, 1988), changes in both density and the proportion of the competing species are evaluated and these experiments are currently the standard for evaluating most species interactions (Silvertown 1987). Research using this experimental design has been conducted in glasshouses (Law and Watkinson 1987, Roush et al. 1989), but field experiments are critical for understanding which plants can be successfully grown together.

Mixture experiments also allow the development of zero growth isolines for populations (Law and Watkinson 1987). These isolines predict the trajectories of various populations over time. In some mixtures, 1 or more species may be driven to extinction (Fig. 4a), whereas other mixtures may develop a dynamic equilibrium (Fig. 4b). Niche differentiation and differential competitive abilities combine to establish distinct positive and negative associations between species as revegetated rangelands develop through time. Aarssen and Turkington (1985) demonstrate this on pastures of differing ages, initially seeded with similar mixtures (Fig. 5). We should expect species that are positively associated over time to coexist when sown in a common seed mixture.

Facilitation, Coexistence, and Resource Partitioning

Seed mixtures of plants having contrasting patterns of above- and belowground growth enhance partitioning of resources in the community and enhance species diversity. Opportunities exist

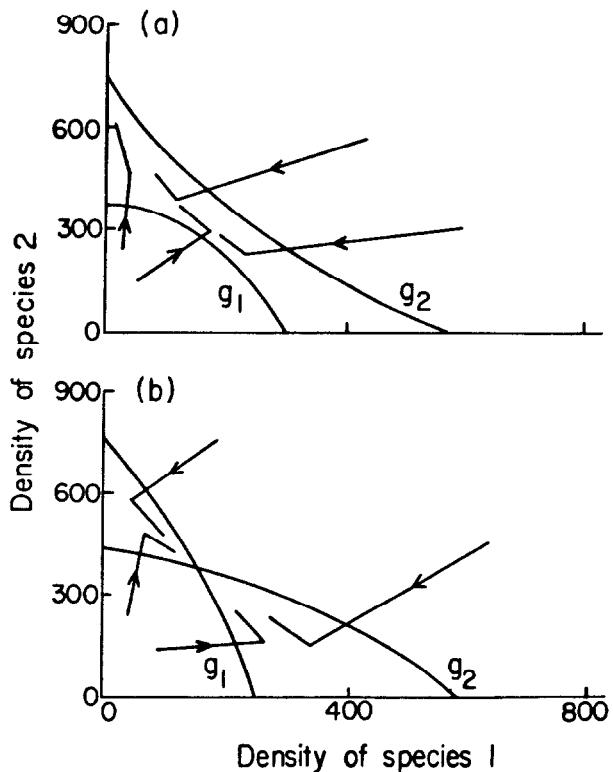


Fig. 4. Zero-growth isolines for a mixture of 2 hypothetical plant species (g_i) illustrating (a) extinction of species 1 and (b) a dynamic equilibrium between the 2 species. Arrows illustrate several possible time-trajectories for species abundances of the 2 populations (adapted from Law and Watkinson 1987).

within herbaceous growth forms to enhance stratification in reconstructed communities. Mixtures of tall-, mid-, and short-height species with C_3 versus C_4 photosynthetic pathways offer an array of combinations that have potential for enhancing productivity, diversity, and coexistence via vertical and temporal stratification of resources.

On impoverished sites with poorly developed nitrogen cycles, legumes may be sown as early colonizers and as a 'nurse crop'. Once a viable nitrogen cycle has been established and conditions are altered so that other species can establish, the importance of these legumes may diminish and they may be outcompeted by the plants whose establishment they facilitated. In other instances, maintenance or addition of leguminous plants in established stands of highly competitive grasses is a management goal, because they improve forage production and forage quality for animals. Legume survival is often temporary in these situations (Rumbaugh and Pederson 1979, McGinnies and Townsend 1983). Persistence of legumes in stands of grass can depend on levels of both nitrogen and phosphorus and can therefore be influenced by fertilization regimes (Barnhisel 1988). However, over the long-term, when competitive abilities of plants are severely unbalanced and when species overlap in resource needs, then the less competitive population is often driven to extinction. Since the potential exists for species to undergo natural selection for either niche differentiation or for balanced competitive ability (Aarssen 1985), it is likely that plant breeders may be able to improve the coexistence of legumes and grasses. This could be achieved by selecting for traits that balance their competitive abilities or for traits that facilitate their partitioning of limiting resources, thus reducing the need for fertilization.

Shrubs and trees encompass an array of morphological and physiological traits that can contribute to vertical stratification of

(a) 1958 Pasture

<u>Holcus lanatus</u>	-----	<u>Dactylis glomerata</u>	-----	<u>Festuca rubra</u>
<u>Trifolium repens</u>	++++	<u>Poa compressa</u>	+++	<u>Taraxacum officinale</u>

(b) 1939 Pasture

<u>Holcus lanatus</u>	-----	<u>Dactylis glomerata</u>
+	+	
+	+	
+	+	
<u>Trifolium repens</u>	++++	<u>Poa compressa</u>
+	+	-
+	+	-
+	+	-
+	+	-
<u>Agropyron repens</u>		<u>Lolium perenne</u>

Fig. 5. Species that were positively (++++) and negatively (----) associated with each other in (a) a pasture sown in 1958, and (b) a pasture sown in 1939 (from Aarssen and Turkington 1985).

resources with grasses and forbs. These lifeforms are often considered undesirable on rangelands because they are presumed to reduce herbaceous production or because their presence increases the difficulty of livestock manipulation. Yet, in many regions or landscapes within a region, woody plants are well adapted to prevailing biotic and abiotic conditions. They play a key role in primary production and nutrient cycling while stabilizing soils, creating islands of fertility (Garner and Steinberger 1989), and providing habitat for wildlife (McKell 1989). The negative connotation associated with woody plants may reflect the fact that woody species with desirable characteristics may have been eliminated or reduced in abundance by excessive utilization or by nonselective brush removal and may have been replaced by less desirable species (Fulbright and Beasom 1987, Welch 1989). Selective inclusion of woody plants in restoration plans offers several potential advantages, including:

- (1) enhanced herbaceous production (Frischknecht 1963 with rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britt.); Christie 1975 with poplar box (*Eucalyptus populnea* F. Muell.); Barth and Klemmedson 1978 with algarrobo (*Prosopis juliflora* (Sw.) DC.); Scifres et al. 1982 with huisache (*Acacia farnesiana* (L.) Willd.); Belsky et al. 1989, Weltzin and Coughenour 1990 with umbrella thorn (*Acacia tortilis* (Forsk.) Hayne);
- (2) enhanced diversity and seasonal productivity of herbaceous vegetation (Ludwig et al. 1988) by creating microclimates suitable for C_3 grasses in areas otherwise dominated by C_4 grasses (Heitschmidt et al. 1986);
- (3) reduced grazing pressure on grasses by providing a refuge for heavily utilized herbaceous species (Welsh and Beck 1976, Davis and Bonham 1979, Jaksic and Fuentes 1980);
- (4) enhanced soil nutrient status (Tiedemann and Klemmedson 1973, Charley and West 1975, Kellman 1979), mineralization (Charley and West 1977), water infiltration (Pressland 1973, Brock et al. 1982), snow accumulation (West and Caldwell 1991).

1983) and vertical distribution of moisture through hydraulic lift (Richards and Caldwell 1987);

(5) improved habitat for wildlife (Parmenter et al. 1985) and soil microbes (Allen 1988, Urness 1989).

The mode of vegetative regeneration of plants sown as a mixture of species may influence the outcome of species interactions. Clonal propagation is ecologically important for several reasons (Jackson et al. 1985): (1) it enables plants in harsh environments to persist until suitable conditions for viable seed production or seedling establishment are encountered; (2) it enables plants to survive shoot damage resulting from grazing, fire, freezing, or drought stress; and (3) the mode of vegetative growth determines how plants exploit space and resource heterogeneity.

Two primary vegetative growth forms of herbaceous plants are caespitose (e.g., bunchgrasses or tussock grasses) and rhizomatous or stoloniferous (e.g., sod-forming grasses). Lovett Doust (1981) has described these contrasting growth form strategies using the terms 'phalanx' and 'guerilla', respectively. 'Phalanx' species are tightly packed advancing fronts of ramets or tillers that restrict other plants from entering their clonal territory. 'Guerilla' species have either long rhizomes or stolons that allow plants to range over large areas of their habitat. Sutherland and Stillman (1988), using foraging theory, have predicted how patterns of plant growth are affected by the environment that is sampled by 'guerilla' species: (1) the probability of branching will be higher in better environments; (2) branch angles will not change in varying environments; and (3) internode length of stolons or rhizomes will decrease with decreasing quality of the environment. Research supports predictions (1) and (2), and in some cases prediction (3).

Plants with caespitose and rhizomatous growth forms are commonly sown together in seed mixtures (Hull 1971, Schuman et al. 1982, Redente et al. 1984, Biondini et al. 1984/85), yet little is known of their interactions. On a given site, will 'guerilla' species spread more rapidly, capture the greatest space, and exploit small-scale variability in resource abundance better than 'phalanx' species? Or will 'phalanx' species more effectively and efficiently garner soil resources than 'guerilla' species? To what extent are these contrasting growth forms compatible and under what conditions?

Species interactions are potential driving forces for successional change. Connell and Slatyer (1977) have proposed 3 models of succession based on species interactions: facilitation, tolerance, and inhibition. In the facilitation model, the entry of new species into a habitat is made possible by other species altering conditions or resource availability. This is particularly true for seed germination and for early seedling survival and is exemplified by the 'nurse plant' phenomenon, whereby established plants protect seedlings of other species from stresses such as grazing, trampling, high temperatures, freezing, and desiccation (Fowler 1986, McAuliffe 1988). Inanimate objects can be used to perform the same functions (Turner et al. 1966, 1969; Steenberg and Lowe 1969). The tolerance model suggests that a predictable sequence of species is produced in a habitat because different species have different strategies for exploiting resources. Species that appear later in succession can tolerate lower resource levels and can grow and reproduce in the presence of earlier species, eventually outcompeting them. Inhibition occurs when a species prevents establishment of other species. Later species gradually accumulate by replacing early individuals when they die.

The above models illustrate that the rate and direction of succession can vary in accordance to the characteristics of the species that inhabit a site. Knowledge of the extent to which certain species may facilitate the ingress or establishment of other species (Yarranton and Morrison 1974; Vasek and Lund 1980; McAuliffe 1984, 1986; Yeaton and Manzanares 1986; Archer et al. 1989; Vitousek and Walker 1989) would be valuable in formulating assembly rules for

ordering the introduction of species into a site. Selective use of species that may behave as inhibitors would produce communities resistant to change. Conversely, selective avoidance of the use of such species in restoration would enable succession to proceed more rapidly.

Conclusion

The rangeland revegetation specialists of the future must become the physicians of the land, broadly trained in the biological sciences with an understanding of the mechanisms that drive ecosystems so that they may prescribe the appropriate treatments for a recovery. We should not depend upon a single species as the cure for degraded rangelands any more than a physician would prescribe the same antibiotic to a single patient for all infections. **Revegetation requires that we examine the rangeland as a physician would examine an ill patient, then prescribe an appropriate treatment for recovery, while at the same time preparing for potential secondary problems (i.e., invasions of weedy species) that may arise in the future. Part of the examination process is recognizing the interactions that take place among plants and between plants and animals (Archer and Pyke 1991) so that an effective prescription can be applied to degraded rangelands.**

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Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland

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Abstract

The role of ungulate grazing in shaping rangeland ecosystems is well known relative to other important plant-animal interactions such as pollination, seed dispersal, granivory, and belowground herbivory. Successful rangeland revegetation may be enhanced by strategies that favor certain groups of animals and discourage others. Many perennial forbs and shrubs require animals for successful pollination, reproduction, and subsequent maintenance of species on a site; however, pollination biology of many rangeland plants and pollinator abundances at potential revegetation sites are largely unknown. Granivory may be significant in some locations and planning and design of revegetation areas may be improved by implementing principles of seed escape mechanisms, such as predator satiation, seed escape in space (low perimeter-to-area ratio for revegetation site), and seed escape in time (synchronous or staggered timing for nearby revegetation sites). Seedling establishment may be associated with invertebrate population levels which need to be considered in future revegetation projects. Timing and site preparation are important in limiting belowground herbivory. Animals can serve as dispersal agents of seeds. Livestock dosed with desirable seeds can disperse them in their dung across the landscape, thereby creating patches of desirable plants. If revegetation sites will be grazed by livestock, then managers should choose plant species that tolerate rather than avoid grazing and should apply adequate management to establish and maintain plant populations. Seeds inoculated with mutualistic species such as mycorrhizae, nitrogen-fixing bacteria, or actinomycetes may enhance establishment, productivity, and nutrient quality of rangeland species while increasing rates of succession.

Key Words: defoliation, granivory, grazing, pollination, revegetation, seed dispersal, seed predation

An awareness of the dynamic interactions between plants and the heterotrophs which use them (e.g., microbes, granivores, frugivores, folivores, etc.) is central to understanding processes that regulate ecosystem structure, population dynamics, the flow of energy and the cycling of nutrients through time (see Crawley 1983). The role of herbivores in shaping ecosystem characteristics via grazing activities has been well-studied relative to other important plant-animal interactions such as microbial associations, pollination, seed predation, and seed dispersal. In our tendency to focus on how grazers modify plant species composition and productivity, we often overlook the reverse consideration that the mixture of plant species or of growth forms may dictate the kind and abundance of animals utilizing a site.

The success of restoration and reclamation efforts may be enhanced by formulating strategies which may favor certain

groups of animals and discourage others. For example, seed predation might be reduced by encouraging animals that prey upon granivores. Providing perching structures for birds of prey might also encourage frugivorous passerines to rest and defecate seeds on reclaimed sites, thereby enhancing plant immigration and species diversity (McDonnell and Stiles 1983, Vander Wall and MacMahon 1984). Strategies to encourage the dissemination of desirable or to discourage the dissemination of undesirable seeds by livestock may also warrant consideration. In a companion paper (Pyke and Archer 1991), we discussed interactions among autotrophic organisms in relation to plant establishment on revegetated rangeland. In this paper, we will address animal impacts on seedling establishment, where the term animal will take a broad definition including heterotrophic microbes such as fungi and bacteria.

Plant-Microbe Associations

The importance of plant-microbe relationships in ecosystem structure and function is widely recognized. In disturbed ecosystems, reductions in plant biomass reduce energy for soil organisms. Microbes associated with plants (rhizosphere organisms), do not, in general, appear to successfully switch from living plant substrates to detritus (Corman et al. 1987, Janos 1988, Perry et al. 1987). As a result, their abundance is linked directly to plant abundance and physiological activity. Reductions in activity of mutualistic or free-living rhizosphere microbes can subsequently influence soil fertility (e.g., by influencing nitrogen fixation) and structure (e.g., aggregate stability [Lynch and Bragg 1985]) and thus, the capacity of soils to store and deliver resources. The absence of microbes (e.g., mycorrhizae) can severely limit seedling establishment, plant growth, and plant survival. As a result, the success of revegetation efforts may be significantly influenced by the extent to which microbial activity in soils has been affected and by the extent to which linkages between plants and soil organisms are subsequently restored (Perry et al. 1989).

Vesicular-arbuscular (VA) mycorrhizae and symbiotic nitrogen-fixing bacteria (*Rhizobium* spp.) or actinomycetes (e.g., *Frankia* spp.) may enhance host and nonhost plant establishment, increase productivity, enhance exploitation of soils for water and nutrients, increase nutrient quality of foliage, and increase rates of succession on reseeded sites (Parker and Chatel 1982, Miller 1987, Allen 1988). These root symbionts may be particularly important to seedlings, which have less storage tissue and smaller root systems than adult plants (St. John and Coleman 1983). Most inferences regarding the importance of root symbionts to nutrient uptake and plant production are based on examinations of surficial roots or on estimations of symbiont abundance in surficial soils. Rhizobial populations are often small or nondetectable under these circumstances; however, inferences based on these criteria may underestimate the importance of microbe-root associations. Large rhizobial populations and viable root nodules may occur deeper in the soil profile (e.g., 2 to 10 m for honey mesquite [*Prosopis glandulosa* Torr.]) where moisture conditions are more favorable and nutrient concentrations rarely reach inhibitory levels (Virginia et al. 1986, Jenkens et al. 1988, Johnson and Mayeux 1990).

Mycorrhizae, rhizobium, and actinomycetes are facultative symbionts that may or may not be present in rangeland soils in

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Authors wish to thank A.L. Aradottir, N. Fowler, T.E. Fulbright, D.N. Ueckert, and S. Zitzer for critical review of earlier drafts of the manuscript; C. Call and B. Roundy for organizing the symposium that brought about our collaboration. Two anonymous reviewers made helpful suggestions which improved the final draft. This paper was partially funded by NSF grant BSR 87-05492, Utah Mineral Lease Funds NR-1181, and Utah Agricultural Experiment Station Project 641 and 891 to DAP and by USDA grants 89-38300-4508 and 89-38300-3625 and Texas Agricultural Experiment Station Project 6717 to SA.

Manuscript accepted 6 May 1991.

adequate numbers and of the appropriate species before reseeding. Levels of mycorrhizal infection can vary significantly between soils (Frankland and Harrison 1985). Erosion and soil disturbances can reduce the inoculation by VA mycorrhizae (Moorman and Reeves 1979, Powell 1980, Allen 1988), and *Rhizobium* (Trinick 1982, Lowther et al. 1987a,b) when native populations of these microbes do exist. Where microbial populations have been substantially reduced by severe disturbance, the probability and rate of spore dispersal into a site will depend on the geographic scale of the disturbance and on the proximity to less disturbed areas which serve as sources of spores (E. Allen 1989). Poor legume establishment on freshly plowed land in western Australia was attributed to soil fungi that produced antibiotics which inhibited *Rhizobium* growth (Holland 1966, Holland and Parker 1966). Plant establishment was enhanced by applying a fungicide or by allowing the field to remain fallow until the fungi became less prevalent.

Site conditions may dictate levels of infection, reproduction, and nutrient acquisition by these microbes. Soil pH influences the success of infection of several species of VA mycorrhizal fungi and *Rhizobium* and influences their saprophytic growth with host plants (Porter et al. 1987a,b, Rice et al. 1977). Post-establishment persistence and spread of alfalfa (*Medicago sativa* L. and *M. falcata* L.) inoculated with *Rhizobium* may depend on seedlings emerging within interplant zones and becoming infected with effective *Rhizobium*. *Rhizobium* density may decrease with increasing distance from inoculated plants, such that soil samples 50 to 100 cm from inoculated plants contain no *Rhizobium* (Lowther et al. 1987b). While seeds inoculated with VA mycorrhizae or with nitrogen-fixing bacteria before dissemination can facilitate plant-microbe symbiosis (Alexander 1977), this technology is available for only a few species (M. Allen 1989).

Establishment and persistence of vascular plants in restoration projects might be facilitated if concentrated efforts were made to introduce free-living nitrogen-fixing bacteria, lichens, or blue-green algae. Cryptogamic crusts may offer particular potential since they enhance surface soil stability, improve water infiltration, and provide pulsed inputs of plant-available nitrogen (Loope and Gifford 1972, Rychert and Skujins 1974, Kleiner and Harper 1977). Establishment of cryptogamic crusts in early stages of restoration may enhance chances for successful seedling establishment and for subsequent plant growth and reproduction (St. Clair et al. 1984).

Pollination

Persistence of a species on a site depends on vegetative regeneration, on the production of new offspring from seed, or on both. Long-lived perennials in arid and semiarid systems may endure adverse conditions and persist by vegetative propagation until the occurrence of a rare window of opportunity for seedling establishment. Allocation of resources to annual flower and seed production may be rather high since the appearance of such windows is unpredictable. Although the resource status of a plant strongly influences its seed output (Stephenson 1981), pollinator service and flower:pollinator ratios may also be important determinants of levels of seed production (Simpson et al. 1977, Silander and Primack 1978, Zimmerman 1980). In some cases, plants may compete for pollinators as well as for light or soil resources (Waser 1978).

Most grasses used in revegetation of rangelands are wind pollinated and are not dependent on animals. In contrast, many perennial forbs and shrubs are insect pollinated and are facultative or obligate outcrossing plants. Cross-pollination is desirable, since the offspring of self-pollinated plants may suffer inbreeding depression. The availability of pollinators for many plants may not be a problem (Bierzychudek 1981, 1982). Pollination success in other cases may largely depend on the presence of a certain insect

species (Augspurger 1980, 1981). The pollination biology of many rangeland plants is largely unknown. In addition, the functional abundance of pollinators on sites slated for restoration may be difficult to determine. In the absence of such information, inferences may be drawn from small-plot experiments where resource limitations to seed production are overcome. If seed production among plants on such plots remains low, the possibility of inadequate pollination should be considered.

Seed Predation

Seeds are subject to predation before, during, and after dispersal (Janzen 1971). The primary granivores of arid and semiarid regions of North America are rodents, whereas in South America, Australia, and Africa ants may be the primary seed predators (Mares and Rosenzweig 1978, Buckley 1982). Levels of seed predation by rodents may be particularly high in disturbed habitats, which may serve as dispersal sinks (Martell 1983). Where granivores are abundant, the composition and spatial pattern of vegetation may reflect seed consumption and the differential distribution of seed predators as well as edaphic variation and interspecific competition (e.g., Bartholomew 1970, Louda 1982, Smith et al. 1989). Rodents and ants have been shown to decrease seed reserves in annual grasslands and desert annual communities by 30 to 80% (Batzli and Pitelka 1970, Nelson and Chew 1977, Borchert and Jain 1978, Reichman 1979, Abramsky 1983). In old-field communities, forb seeds were removed at rates of 3 to 45% per day (Mittlebach and Gross 1984). Seed predation is potentially a major factor contributing to the failure of vegetation establishment when seed is broadcast (Nelson et al. 1970), but drilling of seeds may not insure their escape from predators. Excavation of buried seeds, especially large seeds like vetch (*Vicia* spp.), is known to occur (Reynolds 1950, 1958). Applications of rodenticides and colored dyes have been suggested to reduce seed losses due to rodents and birds during revegetation (Valentine 1989), but these may not be economically feasible.

There are several evolutionary mechanisms which enable seeds to persist in the face of predation. Janzen (1970) has proposed 2 escape mechanisms: escape in space and in time. Escape from predators in space can occur when seeds are dispersed away from parent plants or from cover which may harbor predators (Wilson and Janzen 1972, Webb and Wilson 1985). In planning revegetation areas, a site with a low perimeter-to-area ratio (e.g., large, circular area) will provide escape in space for the majority of seeds by providing a smaller edge from which predators may penetrate the revegetation area. Escape from predators in time can result when seeds are dispersed at unpredictable times or at times when predators are not abundant. Escape can also occur when plants produce more seeds than predators can consume. Known as predator satiation, this phenomenon is exemplified by mast seeding in trees, which appears to correspond to random fluctuations in weather (Silvertown 1980). Predators surviving lean periods between crops will be swamped by food in mast years.

Application of these concepts to revegetation would involve documenting seasonal population dynamics of seed predators to assure that sowing and germination of seeds would occur during periods of low predator abundance. Where adjacent sites are slated for revegetation, seed should be sown in all sites in the same year. This synchronous approach to revegetation will minimize the likelihood that seed predator populations will increase or be maintained over a series of years as might be the case where the same (or a greater) number of seeds are sown in different locations over a series of years. A synchronous approach is similar to the evolved mechanism of synchronous seed production found in bamboo (Janzen 1976). An alternative method of revegetating adjacent sites would be to stagger revegetation so that granivore populations on the treated site return to pre-reseeding levels before nearby sites are

seeded. Providing perching or nesting structures (natural or artificial) for raptors (MacMahon 1987) or approach cover for fox, coyote, bobcat, etc., may help increase predation on granivorous rodents and mitigate their impact. Providing alternative, preferred foods for granivores can reduce the seed consumption of desirable species in the short term, therefore allowing desirable seeds to germinate before predator populations increase. For example, survival of Douglas fir seed was improved from 5 to 50% by providing sunflower seeds in clear-cut areas of forest (Sullivan 1979). Allowances for seed predation should be taken into account when estimating seeding rates that may be required to achieve desired plant densities.

Seed Dispersal

Dispersal of plant propagules (see review by van der Pijl 1972 and Willson et al. 1990) is of central importance in succession and restoration. This is especially true when dealing with large areas where it is not economically feasible to conduct extensive reseeding or when the probability of achieving successful establishment in any given year is low. In such cases, one strategy might be to concentrate resources such that plant establishment is facilitated on smaller patches arranged in a pattern across the landscape. These intensively managed patches could then serve as nuclei of seed production and as future sources of propagules for the surrounding area. Such patches might be initiated from seed or via transplantation of entire plants, plugs, or sods using specialized equipment (DePuit 1988). Groups of tree and shrub species and their associated soils have been transplanted on mined lands using tree spades and front-end loaders (McGinnies and Wilson 1982). Although labor intensive and costly, transplant approaches may ensure ecotypic adaptation, introduction of soil microorganisms, introduction of species that are incapable of rapid establishment from seed, and ensure the establishment of larger plants that are more capable of coping with competition and herbivory.

Moody and Mack (1988) analyzed factors that contribute to the spread of invading plants by simulating various regimes of repeated control. Control regimes included reducing the area of the main stand or destroying some proportion of the smaller satellite stands. Results indicated that spread of species was primarily regulated by the dynamics of satellite stands rather than expansion of the initially large stand. Their simulations suggest that the rate of spread of desirable species might be enhanced by concentrating resources (e.g., seed, fertilizer, and water) to facilitate the development of satellite stands that could subsequently produce seed for natural dispersal rather than spreading those same resources uniformly across an area. Determining the size and arrangement of satellite patches on the landscape falls under the purview of landscape ecology (Neveh and Lieberman 1984, Forman and Godron 1986, Urban et al. 1987) and will not be explored in this paper. A knowledge of seed dispersal patterns and processes would be useful when planning and designing the placement of patches or satellite stands on the landscape. Wind and water are important vectors of seed dispersal for many species. In this paper, we will focus on animals as dispersal agents. Although opportunities exist to utilize wild and domestic animals as agents of seed dispersal to enhance restoration efforts, these must be weighed against negative aspects that may jeopardize the success of the restoration effort (e.g., granivory, dispersal of undesirable species, and excessive herbivory on desirable species).

The relative effectiveness of various agents of seed dispersal are difficult to evaluate, since there is no necessary correlation between numbers of seeds distributed by a particular agent and the value of that form of dispersal (Davidson and Morton 1984). The most effective agent of seed dissemination would transport large numbers of seeds and would deposit them in a germinable form in a microenvironment suitable for establishment. Thus, an animal

that simply transports large numbers of seeds is not necessarily an effective agent of dispersal. Conversely, animals that transport relatively fewer seeds are not necessarily poor vectors.

There is a fine line separating seed predation from seed dispersal in many instances. Seeds dispersed by some animals may escape predation by others. Seeds that escape mastication after ingestion by animals may be regurgitated or survive passage through the digestive tract and be deposited with feces. Ants in some cases (myrmecochory), discard seeds after nutrients have been extracted from external structures (elaiosomes). Granivorous rodents may place seeds in caches where seeds may remain unutilized. Recruitment could be enhanced in each of these cases if probabilities of seed germination and seedling establishment were increased relative to those of undispersed seed.

There are numerous examples demonstrating enhanced germination among seeds manipulated by animals relative to seeds not manipulated (Howe and Smallwood 1982). Enhanced establishment could also be achieved if dispersed seeds were consistently deposited in "safe sites" (Harper 1977). Safe sites for establishment may occur away from conspecific adults which harbor seed or seedling predators or may occur in selected habitats and microsites where resource availability is greater. For example, caching by rodents may result in seeds being buried at depths conducive to germination (Howe 1977), in the placement of seeds in microsites where seedling survival may be enhanced as a result of better light or soil properties, and in escape from seed and seedling predators associated with parent plants (Janzen 1970, Lignon 1978, Webb and Wilson 1985, Howe et al. 1985). Seed-caching or scatter-hoarding by rodents has been implicated as important for Indian ricegrass (*Oryzopsis hymenoides* (R. & S.) Ricker; McAdoo et al. 1983), bitterbrush (*Purshia tridentata* (Pursh) DC.; West 1968), creosotebush (*Larrea tridentata* (DC) Cov.; Chew and Chew 1970, Sheps 1973), *Opuntia* spp. and mesquite (*Prosopis juliflora* (Sw.) DC.) (Reynolds and Glendening 1949, Reynolds 1950), and oak (*Quercus* spp.) and beech (*Fagus* spp.) (Jensen 1985, Miyaki and Kikuzawa 1988). Smith and Reichman (1984) present an in-depth review of seed caching by birds and mammals.

Other factors held equal, recruitment on a site could be increased by increasing the immigration of seeds. This could be achieved in several ways. One approach would be to design the size, arrangement and density of seed-producing "islands" on a site so as to reduce distances seeds must travel. Where animals are important agents of dispersal, provisions for suitable cover and food should be made in reclamation plans. For example, the seed rain of bird-dispersed plants into abandoned fields was increased an order of magnitude when natural and artificial perching structures were provided (McDonnell and Stiles 1983).

Given the large numbers and high concentrations of livestock on many rangelands, their role in seed dispersal warrants specific consideration. Seed dispersal by adhesion (epizoochory) is an evolved adaptation of many low-statured plants of woodlands and disturbed areas (Sorenson 1986), and livestock have contributed to the introduction and spread of exotic weeds via this dispersal method (Benson and Walkington 1965, Mack 1981). Observations of large numbers of seedlings of *Prosopis* and *Acacia* spp. emerging from dung of ungulates have been made on 4 continents (Paulsen 1950, Lamprey et al. 1974, Gutierrez and Armesto 1981, Harvey 1981) and the rapid spread of these hard-seeded legumes is testimony to the effectiveness of livestock as dispersal agents (Brown and Archer 1987). Livestock grazing in autumn or winter breaks inflorescences of crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Shultz.), thereby increasing the potential for germination of seeds retained on the spike by placing them in contact with soil (Pyke 1990). In this example, season of grazing is an important consideration.

Ungulates may also ingest and disperse seeds of a variety of herbaceous species while consuming foliage (Janzen 1984); however, there have been few attempts to use this knowledge of livestock as agents of seed dispersal to aid the establishment and spread of desirable species. Livestock could be strategically fed seeds of desirable species or allowed to graze in areas where the density of desirable, seed-producing plants is high. Once dosed, animals could be released to disseminate seeds into areas targeted for improvement.

This approach, if successful, could potentially offer several biological and economic advantages over conventional reseeding approaches. The most extensive and least expensive methods of seed application (e.g., broadcast seeding) typically meet with the lowest success. Practices ensuring good seed-soil contact are expensive and difficult to apply extensively, especially where brush, rocks, and rough topography predominate. In contrast, a potentially significant proportion of seeds ingested by cattle would be deposited in a moist, nutrient-rich medium that may facilitate germination and establishment. Depending on rate of seed passage and on patterns of animal movement, viable seeds could be distributed over large areas for several days after dosing. The cost of this approach would be relatively low. Emergence of seedlings in dung may occur over long periods, especially where hard-seeded species are involved. The result could be the development of a high density of patches of desirable species that could subsequently serve as local seed sources in the community. For this scheme to work, grazing management would have to be closely regulated, especially at the critical seedling establishment stage, so that livestock did not over-utilize and eliminate the very plants they were spreading.

Major questions relative to actively utilizing livestock as agents of seed dispersal of desirable species pertain to seed survival, to the rate of passage through the digestive tract (a function of seed size, hardness and specific gravity, and of animal diet), to rates of germination in dung, and to subsequent seedling establishment (Fig. 1). Soft-seeded species may lose viability and germinability

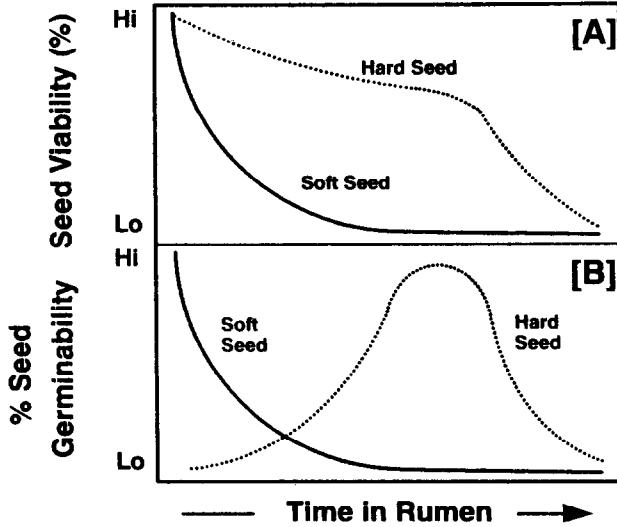


Fig. 1. Hypothetical functions for ingested seeds relating changes in seed viability and germinability to time in rumen.

quickly. Species with hard seed coats may lose viability more slowly. However, seeds passing through the rumen quickly may not be scarified and hence have low germinability. Once scarified in the rumen, additional time in the rumen may be detrimental to seed viability and germinability (Fig. 1). These issues have been addressed to varying degrees for some plant and livestock species (Burton and Andrews 1948, Yamada and Kawaguchi 1972, Welch

1985, Simao Neto et al. 1987, Jones and Simao Neto 1987). Results to date suggest sufficient potential to warrant continued investigation.

Herbivory

Herbivory is the main plant-animal interaction which has been investigated in rangeland ecosystems. Activities of root-feeding nematodes, leaf-chewing grasshoppers, termites, herbivorous rodents, lagomorphs, and large mammals interact with livestock to affect rangeland vegetation. Seasonal and annual fluctuations in the abundance of arthropod and wildlife populations are difficult to obtain. As a result, estimates of numbers of these organisms and of their impact on plants relative to that of livestock is difficult to determine.

The debate over the effects of grazing (positive, neutral, negative) with regard to aboveground net primary production (Belsky 1986, 1987, McNaughton 1986) is often confounded by comparing across levels of organization (e.g., individual plants versus plant communities) and across gradients of resource availability. In addition, the debate may be largely academic for arid and semiarid regions where livestock grazing intensity is usually far in excess of that which might optimize aboveground net primary production (Piper and Heitschmidt 1988). Community-level response to grazing will vary, depending upon the evolutionary history of the species and the systems in which they occur (Milchunas et al. 1988). Plant response to herbivory will depend on an array of interacting factors including the frequency, magnitude, and season of tissue removal; the type of plant part(s) lost; levels of resource availability and competition; and stage of life cycle (Archer and Smeins 1991, Briske 1991). Species-rich plant communities are potentially more resilient than species-poor communities following grazing (Brown and Ewel 1988).

Most research has emphasized the effects of aboveground grazers on vegetation, but belowground herbivores may consume more plant material (Coleman et al. 1976, Stanton 1988). Nematodes, grass grubs (beetle larvae in Scarabaeidae), and scarab larvae (*Phyllophaga crinita* (Burm.)) that consume roots cause significant plant mortality and reductions in shoot production (Ueckert 1979, Detling et al. 1980, Stanton et al. 1981). Estimates of decreased plant production resulting from nematode herbivory range from 6–13% in grassland ecosystems (Ingham and Detling 1984) to 1–10% in agricultural systems (Sohlenius et al. 1988). Aboveground grazing on grasses appears to increase their susceptibility to parasitic nematodes belowground (Stanton 1983, Ingham and Detling 1984). Methods for preparing a site for revegetation that kill the existing vegetation may reduce numbers of belowground herbivores by reducing their food supply. However, if seeds are sown and germinate before reductions in these invertebrate populations occur, or are sown into land with existing vegetation, then these unseen organisms could potentially limit the establishment of seedlings. This is an area of limited research and warrants further study.

Plant adaptations to herbivory fall into 2 major categories: grazing tolerance and grazing avoidance (Table 1). Grazing tolerant plants have characteristics that facilitate the reestablishment of foliage following grazing, whereas plants that avoid grazing have morphological or physiological characteristics (e.g., thorns, secondary chemical compounds) that minimize the probability of defoliation (Archer and Tieszen 1980, Mooney and Gulmon 1982, Briske 1986). Plants with traits conferring grazing avoidance are typically stress tolerators, whereas plants tolerant of defoliation often have characteristics of competitive plants (Pyke and Archer 1991). Trade-offs between competitive ability and tolerance to defoliation may also exist. Windle and Franz (1979) found that cultivars susceptible to insect attack were the superior competitors

Table 1. Characteristics of plants that resist grazing either by tolerating or avoiding defoliation (adapted from Briske 1986).

Grazing tolerance	Grazing avoidance
	Morphological
High number of active meristems present after grazing.	Horizontal leaf and branch angles.
Axillary buds near soil surface or on less preferred branches.	High stem and sheath to leaf blade ratio.
	Prostrate growth form.
	Mechanical defenses — e.g., awns, pubescence, spines and thorns.
	Small foliage elements.
	Physiological
High relative growth rate.	High content of lignin, silica or epicuticular waxes.
High nutrient reserves.	High levels of secondary compounds.
High carbohydrate reserves?	

in the absence of insect pests; when insect interactions occurred, grazing-resistant cultivars replaced the more grazing-sensitive cultivars. The relative merits of adaptations conferring competitive ability versus tolerance to herbivory must therefore be considered in relation to the probability of the plant being defoliated at a given frequency and intensity.

The importance of carbohydrate reserves for regrowth in grazing tolerant plants has been a widely taught concept in range management (Stoddart et al. 1975, Holechek et al. 1989); however, experiments involving dark regrowth of plants and involving grafting indicate that the role of carbohydrate reserves may be less important than shoot characteristics that favor rapid regrowth following grazing (Richards and Caldwell 1985, Fankhauser and Volenec 1989). High frequency, high intensity defoliation of water sedge (*Carex aquatilis* Wahlenb.) tillers over 2 consecutive growing seasons reduced leaf production only on nonfertilized plots, suggesting that nutrients rather than declining plant carbohydrate reserve levels were limiting plant regrowth following defoliation (Archer and Tieszen 1986). Nutrient and moisture limitations to plant growth under field conditions are accentuated by reductions in root initiation, extension, and activity which accompany defoliation (Archer and Tieszen 1983, Richards 1984). Genotypes of perennial ryegrass (*Lolium perenne* L.) with high root to shoot ratios were found by Troughton (1973) to be least sensitive to defoliation, reflecting the importance of roots in plant recovery from grazing. Functional differences in the ability of species to maintain root activity and mass following grazing (Caldwell et al. 1987) are surely an important component of grazing tolerance, but are largely unknown.

Species whose adaptations to the prevailing climate and soils would make them the competitive dominants of the community under conditions of light grazing may assume subordinate roles or face local extinction as grazing intensity increases. Up to a point, grazing may substitute for death or reductions in growth and recruitment that might otherwise be produced by density alone. Grazing may adversely affect plant growth rates, viable seed production, seedling establishment, vegetative regeneration, and plant longevity or survival directly or indirectly (Crawley 1983, Archer and Tieszen 1986). Direct affects are those associated with alterations in plant physiology and morphology resulting from defoliation (Briske 1991). Alterations in microclimate, soil physicochemical properties and plant competitive interactions constitute indirect effects which influence plant response to leaf removal and seedling establishment (Archer and Smeins 1991).

Plants that decrease under grazing do so either because they are intolerant of defoliation or because they are highly preferred and are grazed more heavily than other plants. Inherent morphological

and physiological adaptations for tolerance to herbivory must therefore be evaluated in the context of relative grazing intensity among species in a stand. Plants which are highly tolerant of defoliation will be disadvantaged when competing with associated species which, although less tolerant of grazing, may be defoliated less frequently or intensely (Mueggler 1972, Archer and Detling 1984, Caldwell 1984). For this reason, species chosen for revegetation of rangelands that will be grazed should be dominated by plants with adaptations conferring grazing tolerance. Mixing grazing-tolerant and grazing-avoidance species will inevitably lead to dominance by species which avoid grazing.

Grazing during early stages of seedling establishment may be considered predation based on the strict definition by Thompson (1982) if it causes death of the plant. Seedlings are particularly sensitive to herbivory in that they have low levels of nutrient or energy reserves and shallow, low-density root systems relative to adult plants. Stage of root development is important for anchoring grazed plants. Meadow voles (*Microtus montanus* Peale) are capable of uprooting grass seedlings during the grazing process (Pyke 1987). Species differ in how soon after germination they can be grazed without being uprooted. The desire to have livestock graze plants as early as possible after revegetation has led to the development of grasses such as 'Hycrest' crested wheatgrass (*Agropyron cristatum* (L.) Gaertn. \times *desertorum*). The lateral root production of 'Hycrest' is similar to that of cheatgrass (*Bromus tectorum* L.) (Aguirre and Johnson 1991) indicating that these species may be similar in their ability to resist uprooting while young.

Differences in seed size within and between species affects the rate and timing of germination and the subsequent growth rate and competitive ability of seedlings. There is generally a direct relationship between seed size and seedling performance (Harper 1977). As a result, use of large-seeded taxa with their greater seedling growth rates, may improve chances of establishment in the face of herbivory, competition, and various abiotic stresses. Defoliation can influence subsequent seedling recruitment and stand dynamics by reducing the number and size of seeds that plants produce (Crawley 1983, Jameson 1963, Maun and Cavers 1971a,b).

Because plants are relatively sensitive to defoliation early in their life cycle, deferment of grazing is often helpful, if not necessary, to ensure plant establishment. Deferment during early stages of restoration represents a "cost" in terms of missed opportunity (e.g., loss of revenue) and in terms of expenditures associated with supplementation or boarding of animals elsewhere. However, if grazing too soon after seeding significantly jeopardizes plant establishment, then the restoration effort is doomed to economic failure from the outset. Similarly, the long-term success of a restoration project will hinge on post-establishment grazing management. Plant recovery from grazing can be enhanced while persistence, productivity, and botanical composition can be sustained, but only if proper stocking rates are maintained. This requires matching grazing and rest intervals with the phenology and life history attributes of key plant species (Holechek 1983, Valentine 1989, Heitschmidt and Stuth 1991).

Conclusions

Land managers in the past selected species for revegetation by relying heavily on phytosociological correlations between late-successional species and their environment. Although phytosociology is important in species selection, the land manager of the future should be more like a repair person than a sociologist (Harper 1987). If a piece of equipment is broken, the repair person need not categorize or correlate the equipment (vegetation community) with the place it is used (environment) to fix it. They require a kit of appropriate tools and components and they require a knowledge of the mechanisms that interact in the equipment to

make it work. Land managers require certain tools and components (e.g., plant materials, nutrients, equipment) to use in conjunction with a knowledge of ecosystem processes for successful rangeland revegetation or restoration.

An understanding of plant autecology and plant-environment relationships is crucial to the success of restoration efforts. Biotic interactions, both plant-plant and plant-animal, will operate against a backdrop of edaphic and climatic constraints to further regulate and determine patterns of species distribution, abundance, and persistence over time. Much of our knowledge of the outcome of biotic interactions has come from and will continue to come from attempts to solve applied problems (Harper 1987, Slobodkin 1988) such as those associated with the reconstruction of vegetation communities on disturbed lands. In addition, revegetation and restoration projects offer unique opportunities to investigate species interactions at spatial and temporal scales not generally available in most research environments. Properly designed baseline studies aimed at ascertaining the mechanisms involved in biotic interactions would make a significant contribution to our working knowledge of ecological principles pertinent to rangeland revegetation and restoration.

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Economic feasibility and management considerations in range revegetation

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Abstract

Although range researchers and managers involved in range revegetation often have little economics training, economic analysis is usually a crucial step in range revegetation decisions. This synthesis paper is intended to provide a useful background in economic analysis for teachers, students, and natural resource professionals who deal with range revegetation. First, 3 economic standards by which all revegetation projects must be judged are described and interpreted: (1) economic feasibility, (2) economic efficiency, and/or (3) cost effectiveness. Next, the information required for economic analysis and the analytical procedures used to evaluate range revegetation projects are described. A detailed reseeding example is then used to describe the following information requirements: project costs, benefits, value of benefits, interest rate (including real vs. nominal rates), risk, project life (including life extension and grazing deferment), and range site selected for revegetation. Last, procedures for determining optimal vegetation conversion and use are reviewed, emphasizing the vegetation response function as the key to balancing the 3 determinants of long-term net returns: initial vegetation conversion, grazing intensity, and project life.

Key Words: economic efficiency, economic analysis, vegetation conversion, optimal use

Although range researchers, managers, and others involved in range revegetation often have little formal economics training, economic analysis is usually a crucial step in range revegetation decisions. We offer the following synthesis paper as useful background in economic analysis for teachers, students, and natural resource professionals who deal with the important topic of range revegetation.

Economic Analysis of Revegetation Projects—The General Case

Economic analysis of revegetation projects involves judging such projects by 1 or more of the following economic standards: (1) economic feasibility, (2) economic efficiency, and/or (3) cost effectiveness.

Economic Feasibility—Will the Project “Pay”?

Mathematically, economic feasibility could be called the *necessary* condition for maximum net returns (Workman 1984). A project is said to be economically feasible if it yields a positive net return (i.e., discounted returns exceed discounted costs). An economically feasible project has a net present value ($NPV \geq 0$), a benefit/cost (B/C) ratio ≥ 1 , and an internal rate of return ($IRR \geq$ the appropriate discount rate (Workman 1986). A positive NPV indicates feasibility because the project yields a positive net return (a profit) after paying all costs, including interest on borrowed capital. A B/C ratio greater than 1.0 indicates feasibility because discounted benefits exceed discounted costs (i.e., more than a dollar is returned for each dollar invested). An IRR greater than the

interest rate on borrowed money indicates feasibility because the discount rate that forces future net returns to equal the present investment exceeds the borrowing rate.

Economic Efficiency—the “Biggest Bang for the Buck”

Mathematically, economic efficiency could be called the *sufficient* condition for achieving maximum net returns (Workman 1984). A project is considered to be economically efficient if it represents the most productive use of available capital and other required inputs. Thus an economically efficient project yields a higher net return than any other potential use of limited capital (i.e., an efficient project promises the “biggest bang for the buck”). Not only is the NPV for an efficient project *positive*, it is the *maximum* NPV possible from available capital.¹

Cost Effectiveness—a “Specified Bang for the Smallest Buck”

No range manager has sufficient budget to implement *all* biologically sound and economically feasible improvements on rangeland under his/her control, and a choice must be made from among those available. These decisions are further complicated by what have been termed “critical projects” (Workman 1986), i.e., those considered necessary even though they are not economically feasible. As an example, suppose there is a highly visible public range “sore spot” in the form of a steep area that has become denuded of vegetation and highly eroded by indiscriminate off-road vehicle use. Even though it is agreed that the monetary returns from revegetating the area will be far less than the costs, it is also agreed by the land management agency (and the public observing its actions) that the area *must be* reclaimed. Even in this example, where few people would argue that revegetation was unnecessary, public monies are to be used to fund the project and the agency is obligated to seek a “least-cost” method of revegetation. What began as a biological problem has become an economics-based decision.

Range revegetation efforts are also sometimes made in response to legal requirements that the land be reclaimed. Thus no decision is required concerning whether or not revegetation *will be* done. However, economic analysis is still a crucial part of the decision of *how* to accomplish the revegetation goal. Whether public land to be revegetated with public funds or private land to be reclaimed through private investment, the problem is simply to find the least expensive means of achieving the desired revegetation. Instead of searching for the “biggest bang for the buck” as described above, cost effectiveness analysis² tries to produce “a specified bang for the smallest buck” (Workman 1984). While crucial, the required economic analysis for the cost effectiveness case might be quite short. In its simplest form such an “analysis” might consist of only a statement that several proven methods are available to achieve the required revegetation and that the least expensive of these will be used.

¹Note that NPV here, like NPV in Economic Feasibility above, is calculated as the difference between returns and costs, both discounted at the *borrowing rate*. If discounting is done, instead, at the *opportunity cost rate* (the rate of return on the best alternative use of capital), then the resulting *one* project that yields a positive NPV is the economically efficient project.

²The term cost effectiveness analysis is defined here as analysis used to select the minimum cost method of accomplishing a goal that has already been set (Howe 1971). This standard definition should not be confused with the use of the term “cost effective” by U.S. Forest Service (1980) as a synonym for the term “economically efficient” discussed above.

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Supported by the Utah Agricultural Experiment Station, Utah State University, Logan 84322-4845. Approved as journal paper 3880.

Manuscript accepted 6 May 1991.

Information Required for Analysis

Information concerning the following items is required for economic analysis of range revegetation: (1) project costs, (2) project benefits, (3) value of benefits, (4) interest rate, (5) project risk, (6) expected project life, and (7) the range site selected for revegetation. Each of these factors influences economic feasibility and efficiency.

Project Costs

Expected costs of range revegetation include both initial project investment and induced operating and maintenance costs. The main revegetation costs often consist of the initial investment in soil preparation, seed, and seeding. However, when revegetation is done primarily to enhance livestock forage production and allow breeding herd expansion, the induced costs of increasing the herd (whether purchased or retained from homegrown young stock) may exceed the initial costs of revegetation, itself (Workman 1986). Other important revegetation induced costs include construction and maintenance of fences and stock water facilities required to control grazing on reclaimed areas. These induced costs can be an important determinant of the economic success of revegetation efforts. Kearn and Brannan (1967) found, for example, that differences in fencing requirements for vegetation conversion projects can cause a 300% variation in per hectare treatment costs on small tracts of land. The crucial influence of grazing deferment cost on the economic feasibility of revegetation is examined in detail below. In the range reseeding example to follow (Table 1) initial investment consists of 6.7 kg/ha of Fairway crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) seed at \$2.67/kg and plowing and seeding costs of \$39.54/ha, a total initial investment of \$57.43/ha (USDA 1984).

Project Benefits

Some revegetation projects primarily yield stable soils and watersheds and their most important benefits might best be measured in terms of decreased erosion and improved water quality. But often the most important quantifiable impacts of reclamation efforts are increases in quantity and quality of livestock forage. The forage benefits lead to (1) increased yearlong carrying capacity, allowing herd expansion, and (2) reduced per animal feed costs since range forage can be substituted for more expensive harvested or purchased feeds.

Suppose the area to be revegetated is rangeland classified as the Upland Loam range site and is currently in poor condition. Current herbage production is 1,318 kg/ha (1,176 lb/ac), the average of 715 kg/ha (638 lb/ac) and 1,921 kg/ha (1,714 lb/ac) reported by Mason (1971) for poor condition (Fig. 1). Suppose further that

seeding the area to an introduced cool-season grass such as crested wheatgrass will increase herbage production to 1,511 kg/ha (1,348 lb/ac), the average of 1,009 kg/ha (900 lb/ac) and 2,013 kg/ha (1,796 lb/ac) for good condition (Fig. 1). In poor condition, only 23% of the total plants on this site are forage species (Fig. 1). If forage utilization is 50%, 152 kg/ha of usable forage are produced annually (Table 1). If the animal unit month (AUM) requirement is 300 kg (National Research Council 1970), this site in poor condition has a carrying capacity of 0.51 AUM/ha. If the seeded stand results in 90% forage species, the carrying capacity is 2.27 AUM/ha, a 1.76 AUM/ha increase over that before seeding (Table 1).

Value of Benefits

The next step in the economic analysis of our reseeding example is to assign a value to increased carrying capacity. Several analytical techniques have been used to estimate the dollar value of increased forage. These techniques may be grouped into 2 categories: (1) complex approaches that estimate the value of increased livestock production made possible by additional AUMs and (2) simple approaches that value additional AUMs of forage in terms of lease price.

Value as Increased Livestock Production

Valuing revegetation benefits in terms of increased livestock production requires tracing the impacts of increased seasonal forage (spring-fall carrying capacity in our reseeding example) on yearlong forage balance and the resulting increase in yearlong breeding herd carrying capacity (Workman and MacPherson 1973). It also involves the use of "partial budgeting" to determine the resulting added annual livestock returns, added annual livestock operating costs, and added initial investment, including increasing the size of the breeding herd (Workman 1986, Cook and Stubbendieck 1986, and Scifres 1987). *Budgeting* is a simple procedure to estimate the effects of production changes on costs and returns (Caton 1957). In *partial* budgeting, the costs and returns that are not affected (taxes, insurance, depreciation) by proposed management changes are omitted from the calculations (Cook and Stubbendieck 1986).

This process of valuing increased forage production has become much easier and faster as partial budgeting "by hand" has been replaced by spreadsheets, linear programming (LP), and other optimization techniques applicable to range improvement decisions. While noncomputer-assisted partial budgeting can deal with only 1 proposed improvement at a time, LP can calculate the optimum combination of potential range improvement practices (Jameson et al. 1974). Kim (1971), Beneke and Winterboer (1973),

Table 1. Comparison of per hectare costs, increased production, increased annual return, and net present value (20-year life, 9% interest) due to seeding 2 range sites.

Upland Loam Range Site											
	Herbage (Kg/Ha/ Yr)	Forage %	% Utiliza- tion	Forage (Kg/Ha/ Yr)	Req. forage (Kg/ AUM)	Car. cap. (AUM/ Ha)	Incr. prod. (AUM/ Ha)	Ann value incr. prod. (\$/Ha)	PV incr. prod. (\$/Ha)	Init. inv. (\$/Ha)	NPV (\$/Ha)
After seeding	1511	90	50	680	300	2.27					
Before seeding	1318	23	50	152	300	.51	1.76	14.94	136.37	57.43	78.94
Upland Shallow Loam Range Site											
After seeding	1288	90	50	580	300	1.93					
Before seeding	599	27	50	81	300	.27	1.66	14.09	128.62	57.43	71.19

YIELD AND VEGETATION COMPOSITION

Upland Loam Range Site

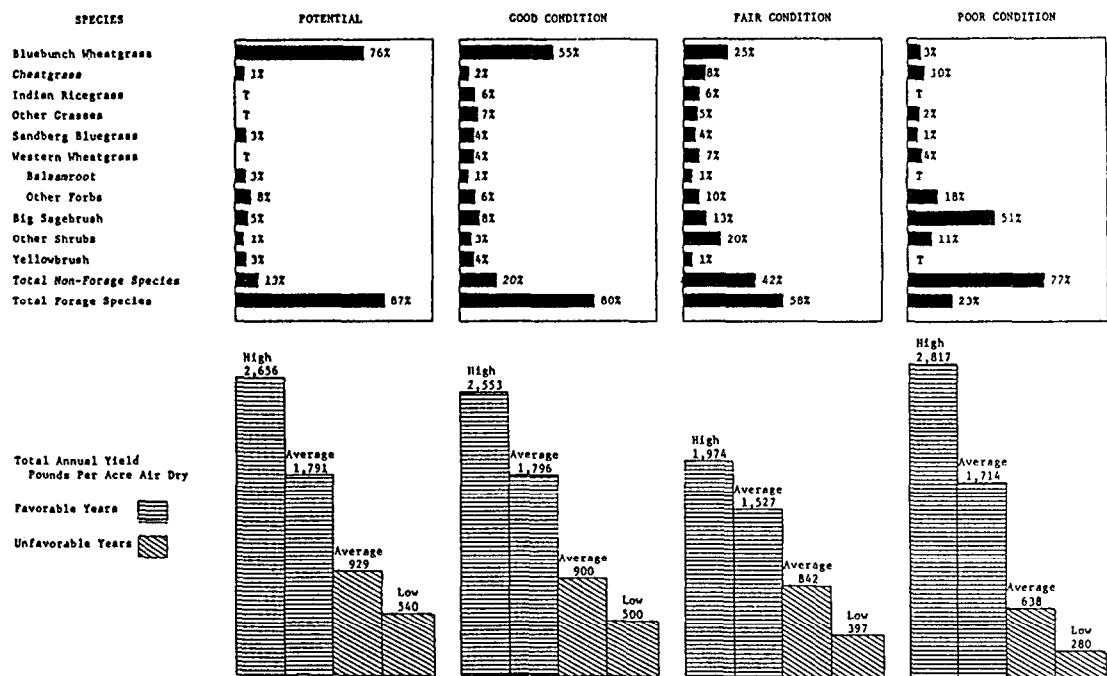


Fig. 1. Yield and composition, Upland Loam range site (from Mason, 1971).

and Jameson et al. (1974) provide detailed discussions of the mathematics involved. Examples of LP applications to range vegetation conversion or revegetation decisions include Sharp and Boykin (1967), Child and Evans (1976), and Tanaka and Workman (1988).

It is sometimes comforting to range professionals who haven't studied economics to be reminded that LP is based on traditional procedures of partial budgeting (Workman 1986). The computer only makes the process faster and easier and allows numerous production constraints (i.e., seasonal forage, labor, borrowed capital) to be analyzed simultaneously.

Space does not allow a demonstration of valuing revegetation benefits in terms of increased livestock production. Several detailed examples of this procedure are available in the literature (Workman 1986, Cook and Stubbendieck 1986, Tanaka et al. 1987, Valentine 1989).

Value as Leased Forage

Valuing revegetation benefits as privately leased forage is simple and straightforward. In many cases this approach yields accurate estimates of the value of increased forage from revegetation, particularly in situations where the land owner currently leases forage from other rangeland owners and can avoid paying future lease fees by revegetating his/her own rangeland (Workman 1986). Even a land owner not currently involved in leasing usually has the opportunity to lease increased private forage to neighboring operators so pricing increased forage production at the private lease rate is valid.

It should be noted that pricing at the private lease rate often yields a higher revegetation benefit than does valuation as increased livestock production (Workman 1986). It should also be noted that published private lease rates include a premium for

landlord services of about 30% (Torell et al. 1989a) and that the value of additional forage, itself, is only about 70% of published lease rates. However, for simplicity in the following reseeding example, increased forage will be valued at \$8.49 per AUM. This is the average private lease rate for the 16 western states, 1985-87 (USDA 1988).

Interest Rate

Real Versus Nominal Interest Rates

Calculation of NPV of our reseeding project requires that all future costs and benefits be discounted to the present. Care must be taken to express all prices and interest rates in consistent terms, either all *real* or all *nominal* (Howe 1971, Overton and Hunt 1974, Hanke et al. 1975). In economics parlance, a real price is one that is inflation-free while a nominal price includes inflation.

The above \$8.49 per AUM value is a real price. It is projected into the future, over the entire life of our reseeding, in constant 1987 dollars. For consistency, since inflation is not included in future benefits, neither should it be included in the discount rate. So this *real* future flow of revegetation benefits must be discounted at a *real* interest rate. Borrowing rates charged by lending institutions are expressed in nominal terms. A 10% rate quoted by a bank for a reseeding loan is the sum of the bank's required *real* rate of return, say, 4% and an expected *inflation* rate of 6%. A real borrowing rate, then, is calculated by subtracting the expected inflation rate from the quoted nominal borrowing rate.

Alternatively, both revegetation benefits and the discount rate could be expressed in nominal terms. This would involve combining the *known* (quoted) nominal borrowing rate (10% in our example) with *predicted* future nominal forage prices over the life of the reseeding project. Due to the tendency for fluctuating live-

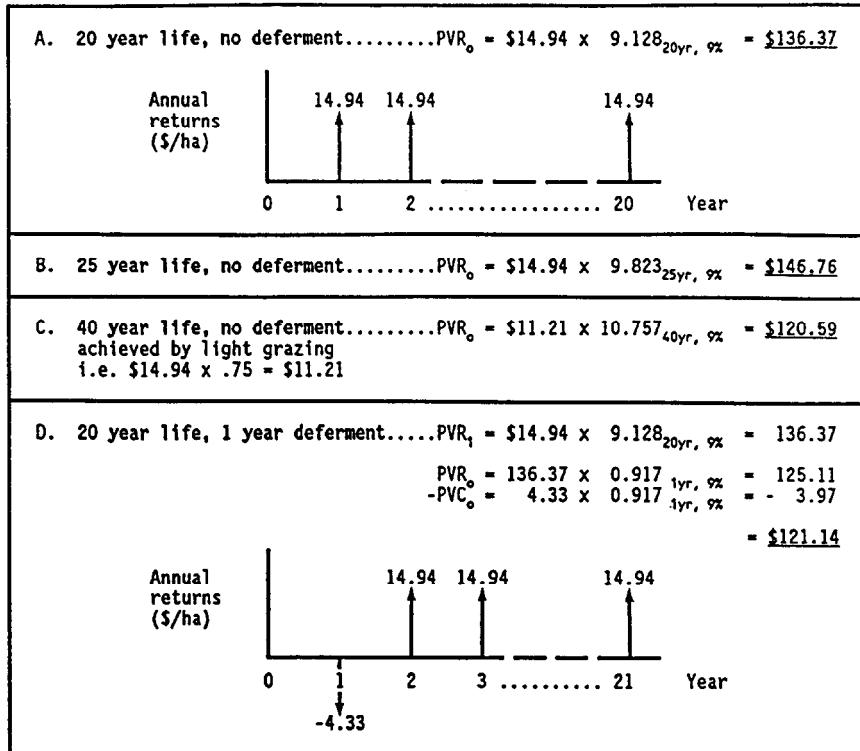


Fig. 2. Effects of extending the useful life and of requiring a 1-year grazing deferment on the present value of annual returns to range revegetation.

stock prices not to keep pace with general inflation trends, some researchers believe that projecting *current* livestock prices over project life yields a measure of *nominal* project benefits (Ethridge et al. 1987). Both the nominal and the real approaches are correct, provided that they are kept consistent. For analysis of our reseeding example, we will combine the real forage price of \$8.49 per AUM (USDA 1988) with a risk-free real discount rate of 4% (Row et al. 1981).

Risk

Many range revegetation projects involve some degree of risk. Numerous factors can cause actual results to deviate from those expected. Due to variability in weather and price alone, results can seldom be predicted with complete certainty (Cook and Stubben-dieck 1986).

In everyday usage, "risk" describes any departure of actual from expected results. For economic analysis, however, risk should be further divided into "risk" and "uncertainty" (Cook and Stubben-dieck 1986). The probabilities of occurrence of some events (e.g., a severe drought) can be calculated, based on records of the past. This is true "risk". The probabilities of other events (e.g., livestock prices in a freely fluctuating market) cannot be calculated. This is "uncertainty". Various attempts to deal with the risk and uncertainty of range management and range improvements are detailed in the literature (Whitson 1975, Banner 1981, Whitson et al. 1982, and Walker and Helmers 1983).

Economic analysis of range revegetation or vegetation conversion must include risk since the probability of biological success or failure can affect economic results as much as any factor considered here (Tanaka and Workman 1989). It is much easier, of course, to incorporate risk than uncertainty. We will deal only with risk in our reseeding example.

Suppose that based on past reseeding records for the Upland Loam site we calculate the risk of seeding failure to be one failure

out of 20 seedings (5%). In the literature, such risk has been incorporated into the analysis in 2 ways. First, risk can be included by adding a risk premium to *initial investment* (Row et al. 1981) and then discounting real returns and costs using a *risk-free* discount rate. In our example, this would require adding 5% to our \$57.43/ha initial investment, resulting in a risk-included initial investment of \$60.30/ha. Or, second, real returns and costs can be discounted using a *risk-included* discount rate (Arrow and Lind 1970, Howe 1971) and no risk premium added to initial investment. In our example, this would require adding the 5% risk rate to the 4% real borrowing rate to give a real risk-included discount rate of 9%. We will analyze our reseeding example using this second approach.

Project Life

Migration of less desirable vegetation into a seeded or converted area is usually a gradual but almost inevitable process. While revegetation benefits do not end abruptly, a time may come when forage production and livestock carrying capacity return to their pre-treatment rates. While estimates of benefit duration are subjective, at best, such estimates must be made in economic evaluation of revegetation and should be based on research results and management experience on the range site to be treated (Workman 1986). The dynamic impacts of this process are discussed in the optimal vegetation conversion and use section below.

Life Extension

Traditionally, range managers have been conservative in estimating expected project life. It is common to view a 30-year-old range seeding where the drill rows are still plainly visible and to learn that at the time of establishment its useful life was projected to be 20 years. But these conservative projections by range professionals do not do violent damage to the accuracy of economic analysis. Suppose that we *projected* a 20-year life (Fig. 2A) for the Upland Loam seeding of Table 1 but the *actual* life was 25 years

(Fig. 2B). This 5-year under-estimate reduces present value of annual returns (PVR_o) by only \$10/ha (from \$146.76/ha to \$136.37). It is comforting to note that under-estimating project life results in a proportionately smaller under-estimate of PVR_o . Much less comforting is the fact that extending the life of an already long-lived project is also not worth much in present dollars. A 5-year (25%) life extension (from 20 to 25 years) adds only \$10 (8%) to PVR_o . Of course, if the seeding life could be extended 5 years at no cost, that would be great. But project life extension is not free. Suppose seeding life could be doubled from 20 to 40 years if annual grazing use were reduced 25%. How would this affect the economic outcome of the project? Doubling project life in this case actually reduces PVR_o by about \$15/ha (from \$136.37/ha in Fig. 2A to \$120.59/ha in Fig. 2C). The important conclusion is that extending an already long-lived project is not worth much in discounted dollars.

Grazing Deferment

Since adding distant-future years to expected life is worth so little in discounted dollars, perhaps it is not surprising that subtracting near-present years from expected life is very costly to economic feasibility. This is best demonstrated by requiring a grazing deferment for our reseeding example. Deferments were not required for the seedings portrayed in Fig. 2A, 2B, and 2C. These cases are based on seeding in the fall after normal spring-fall grazing is completed and then returning to graze the following fall after the seeding has completed 1 full growing season. Now suppose that we require complete grazing deferment during the entire year after seeding. Deferment brings 2 changes to the "flow" of reseeding benefits over time (Fig. 2D). First the initiation of production response is postponed from year 1 to year 2. This 1-year change reduces PVR_o by \$11/ha (from \$136.37/ha to \$125.11). Second, an alternative forage source must be found to replace the

pre-treatment carrying capacity not available during year 1 (Nielsen 1984). The value of this alternate forage is $0.51 \text{ AUM}/\text{ha}$ (from Table 1) $\times \$8.49/\text{AUM} = \$4.33/\text{ha}$ and must be treated as a cost in year 1. This alternate forage must come from either owned land (in which case the opportunity to devote this forage to other uses is forgone) or must be leased from a neighboring landowner at the going private rate. In present dollars, this alternate forage costs \$3.97/ha seeded (Fig. 2D). Combined, the 2 changes due to grazing deferment reduce PVR_o by \$15/ha or 11% (from \$136.37/ha to \$121.14).

Imposing a year of grazing deferment brings a substantial reduction in revegetation PVR_o . Is there anything positive that can be said about required deferment of reseeded areas? Happily, yes, and it's simply this: there is probably no greater contribution that a range professional could make towards improving economic feasibility of revegetation than to develop ways to ensure revegetation success with less required deferment.

Range Site Selected for Revegetation

In almost any range revegetation or vegetation conversion decision, the amount of land that would respond to treatment far exceeds the amount that can be treated with the available budget. So the range manager must often first decide how much of which range site(s) to revegetate. Range managers have sometimes tended to concentrate their limited improvement budgets on the worst sites (the most fragile and least productive and responsive) because "these worst sites need improvement more" than the best sites (those most resilient, productive, and responsive). Unfortunately, this "worst first" thinking confuses what we might like to do with what we can afford and can cause serious errors in allocating revegetation budgets between sites. Instead, if our goal is to maximize response (revegetation success, increased forage, and increased

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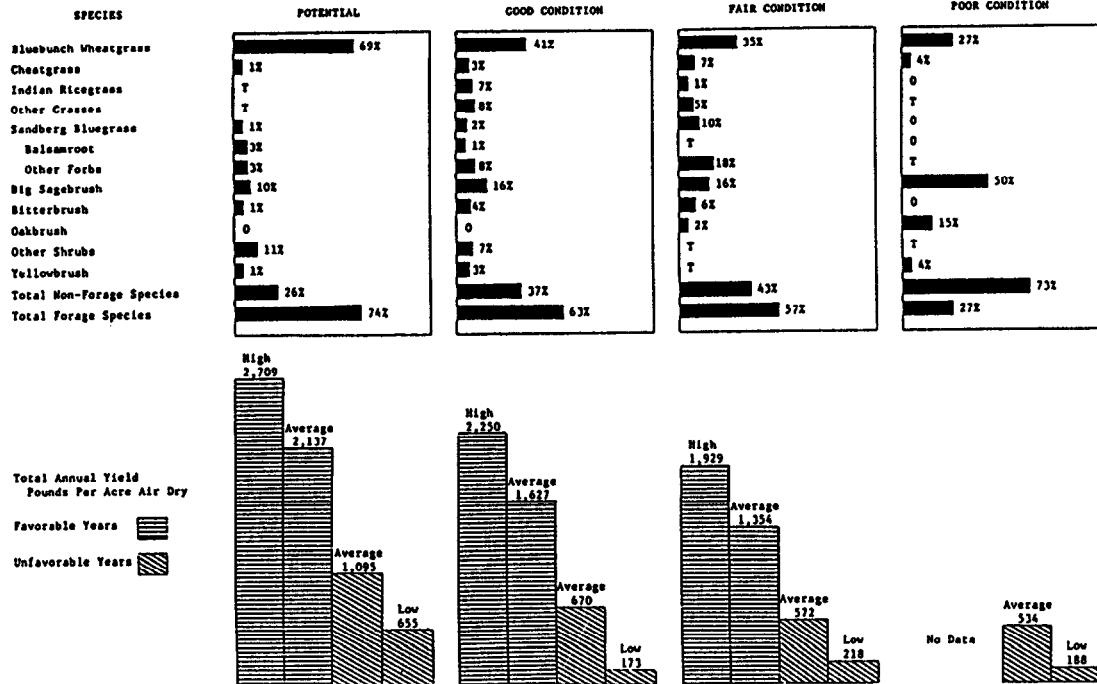


Fig. 3. Yield and composition, Upland Shallow Loam range site (from Mason, 1971).

annual returns) to limited revegetation budgets, time, and other resources, we should treat our *best* sites first (Workman 1986). We will use the information in Figures 1 and 3 and Table 1 to demonstrate this important rule.

Nielsen and Hinckley (1975) observed that there is often a direct relationship on a particular rangeland area between pretreatment and posttreatment forage production. This relationship is apparent in Table 1 for our reseeding example. In poor condition (before seeding), forage production of the Upland Shallow Loam site is less than on the Upland Loam (Fig. 3 compared to Fig. 1). The Upland Shallow Loam site is also less responsive to reseeding. The same reseeding treatment (Table 1), with the same initial investment of \$57.43/ha produces a larger forage production increase on the Upland Loam than Upland Shallow Loam (1.76 AUM/ha versus 1.66 AUM/ha). While this 0.1 AUM/ha difference might appear small, the resulting \$8/ha difference (\$78.94 vs. \$71.19) in Net Present Value (NPV = PVR_o - Initial Investment) is not.

Reseedings on both sites are economically *feasible* since both yield a positive NPV (Table 1). The PVR_o calculations in Table 1 (and Fig. 2) are based on the borrowing rate. As mentioned above, ideally the discount rate should be the higher of either the borrowing or the opportunity cost rates. However, because the opportunity cost (in this case the rate of return on the best alternative use of capital required for the reseeding) is not always known, economic analysis of range improvements is often based on the borrowing rate (Workman 1986). If the only alternative use of funds required to reseed the Upland Loam site were to reseed the Upland Shallow Loam site, we can conclude that, in addition to being economically feasible, our Upland Loam seeding is economically *efficient* (it yields the highest possible NPV). We can conclude that our Upland Shallow Loam seeding, while economically feasible, is *not* economically efficient since we know of at least 1 other use of the required funds that will yield a higher NPV (seeding the Upland Loam).

Optimal Vegetation Conversion and Use

Consistent with the economic efficiency goal discussed above, vegetation conversion must be implemented at a level that will maximize net returns (however measured). In order for this to occur in a long-run dynamic setting, there are 3 important vegetation conversion variables that must be included in the analysis. These are the long-term response function, project life, and expected use of the treated area.

The ranch or grazing allotment forms the analytical basis for economic analysis of vegetation conversion. If vegetation conversion is intended to reverse declining range condition (desertification) on private (or public) land and the rancher (or public land manager) has the goal of maximizing net returns (or net benefits to society) from limited investment funds, we need to answer 4 questions: (1) What percentage of the undesirable vegetation should be targeted for removal? (2) How many hectares should be treated? (3) What should be the grazing intensity on the treated area? and (4) How often should the area be retreated (i.e., what is the optimal project life)?

Numerous analytical methods have been used to determine economically optimal vegetation conversion practices. These have varied from relatively simple static methods to decidedly more complex dynamic methods (Dykstra 1984). No matter what method is used, the same information is required but is used differently. The most important variable is the long-term response function. In the static case, an average treatment response is assumed over the life of the project, holding all else constant. In the dynamic case, response changes over time as a function of initial treatment level, grazing intensity, and random effects (e.g., weather).

The simplest method (and probably the one that has been used

the longest) is linear programming (LP). Even though LP can optimize management inputs for maximum net returns, it cannot adequately address the above questions. This has led to the use of increasingly complex models in problem formulation. Bernardo and Conner (1989) have discussed the advantages and disadvantages of applying several more complex methods (e.g., dynamic programming, optimal control theory, expert systems) in range economics. However, in most instances we do not have enough information on long-term response functions to reliably use these methods so we are left with 3 compromises: (1) do nothing while waiting for more data, (2) make educated guesses about the response function, or (3) rely on simpler methods and attempt *near-optimal* solutions while recognizing the inherent limitations of these methods.

The literature reveals some general "rules" that apply to revegetation and subsequent management from an economic perspective. First, the more complete the removal of an undesirable overstory species, the greater the initial investment cost, understory species response, and project life. Studies on many U.S. vegetation types have shown a convex relationship between understory production and overstory reduction percentage (Tanaka 1986). Second, the heavier the grazing intensity on a revegetated stand, the shorter its life but the greater the NPV. As explained above, this is due to the fact that returns received early in the project life have a much higher present value than returns received far into the future. Third, the number of hectares treated must be balanced with the expected vegetation response and the value of additional forage during the season of the year when available for grazing. In order to optimize vegetation conversion inputs for maximum net returns, all of these "rules" must be balanced together.

The theoretical basis for optimal overstory reduction on big sagebrush (*Artemesia tridentata* Nutt.) sites revegetated with crested wheatgrass (*Agropyron cristatum* (L.) Gaertn., *A. desertorum* (Fisch. ex Link) Schult.) has been examined by Torell (1984) and Tanaka (1986). Case studies applying the theoretical model have also been developed (Tanaka and Workman 1988, 1990; Torell and McDaniel 1986; Torell and Hart 1988; Torell et al. 1989 b, c). The interactions among decision "rules" described above were evident in the reported results. For example, if grazing intensity of crested wheatgrass was held constant, optimal (maximum NPV) big sagebrush reduction was 92 to 100% for a specified project life (Tanaka and Workman 1988). If grazing intensity was increased, however, project life would be shortened (Torell 1984). The overall goal is to find the balance of the 3 factors (initial reduction percentage, grazing intensity, and project life) that will lead to maximum NPV over an infinite time horizon.

Continuing with the seeding example, we will expand the analysis to consider the dynamic aspects of the problem. A dynamic production function is affected by both the amount of initial overstory removal and subsequent utilization rate (Fig. 4). The value of the forage produced, cost of the vegetation conversion, and interest rate remain the same. In the dynamic case each year's benefits must be discounted individually. Adding these values together over the life of the project results in PVR_o as before.

The static and 3 dynamic cases are illustrated in Figure 4. The first dynamic case (D-50-95) assumes a 50% utilization rate and 95% initial overstory removal. This results in a 20-year project life due to big sagebrush encroachment into the stand. If we decide to stock heavier and achieve a 75% utilization, we will obtain more forage in early years of the project but there will be a project life of only 15 years (D-75-95). If the goal of the conversion project were to leave half the sagebrush for other resource uses and stock at 50% utilization (D-50-50), we expect more than 50% reduction in usable forage due to the convex shape of the projection function and a more rapid stand deterioration (i.e. project life of only 10 years).

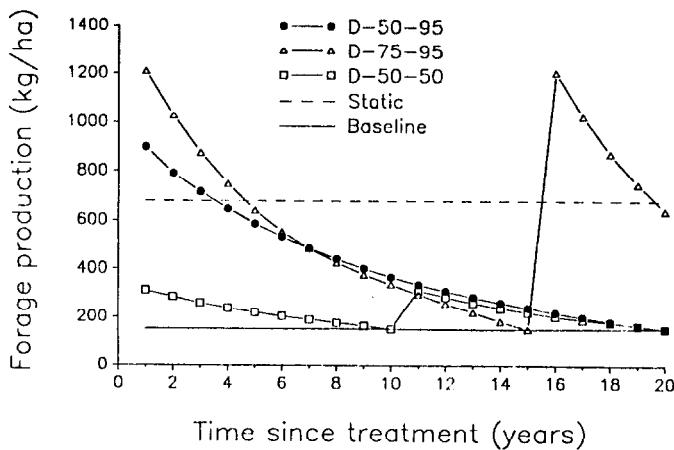


Fig. 4. Hypothetical dynamic (D) and static production responses of crested wheatgrass on an Upland Loam range site under alternative utilization rates (50 or 75%) and initial big sagebrush kill rates (95 or 50%). Baseline is forage production on the site in poor condition.

We can compare the PVR₀ to initial investment costs (Table 2). Initial treatment costs for D-50-95 and D-75-95 are the same as in the static case (\$57.43/ha). The lower kill rate for D-50-50 results in lower treatment costs. If all projects are put on a 20-year basis (assuming treatments can be repeated as shown in Fig. 4), we can make some economic comparisons. Note that the cost of the repeat treatments in D-75-95 and D-50-50 have been discounted (Table 2).

Table 2. Comparison of per hectare discounted costs and benefits and net present value (9% interest) of static and dynamic vegetation conversion projects on the upland loam range site.

Year	Conversion project			
	Static	D-50-95 ¹	D-75-95 ²	D-50-50 ³
0	-57.43	-57.43	-57.43	-47.43
1	13.71	19.42	27.47	4.17
2	12.58	15.22	20.90	3.18
3	11.54	12.33	15.83	2.36
4	10.59	9.96	11.95	1.74
5	9.71	8.02	9.01	1.26
6	8.91	6.44	6.80	0.90
7	8.17	5.15	5.14	0.61
8	7.50	4.10	3.89	0.37
9	6.88	3.26	2.94	0.17
10	6.31	2.57	2.21	-20.03
11	5.79	2.02	1.58	1.76
12	5.31	1.58	1.07	1.34
13	4.87	1.21	0.64	1.00
14	4.47	0.92	0.28	0.73
15	4.10	0.68	-5.25	0.53
16	3.76	0.48	7.54	0.38
17	3.45	0.32	5.74	0.26
18	3.17	0.18	4.35	0.16
19	2.91	0.06	3.28	0.07
20	2.67	0.00	2.47	0.00
NPV (\$/ha)	78.94	36.51	70.39	-46.37

¹Dynamic, 50% utilization, and 95% initial kill.

²Dynamic, 75% utilization, and 95% initial kill.

³Dynamic, 50% utilization, and 50% initial kill.

Increasing the stocking rate to 75% and accepting a shorter project life is the best dynamic alternative analyzed (Table 2). However, even this best dynamic project has a lower NPV than that determined for the static case. The reason for this is evident in

Figure 4. The static case uses a constant production level while the dynamic cases show rapid declines in forage production. Although 2 of the dynamic cases start out with higher forage production levels than the static case, both decline rapidly, giving lower NPVs.

Reducing initial overstory kill to 50% (D-50-50) results in a negative NPV and this case would not be considered economically feasible. If the goal were to leave some sagebrush in an area, an alternative to D-50-50 would be to create a mosaic pattern—leaving some areas alone while striving for maximum overstory removal on others. Due to the convex shape of the production function, this might also require fewer acres to be treated to achieve the same forage production increase.

To summarize, economic optimization of vegetation conversion requires long-term data. This need has been recognized in the economics literature for many years (Martin 1972, Bernardo and Conner 1989) but the required data have not been collected. Apparently, these important long-term studies have not been favored by either research sponsors or by individual researchers. The few data sets that have been collected on the same site over a period of years have been fragmented through time and confounded by many environmental and management changes. The solution to the "not data" problem is either to conduct such studies over entire project lives on many different sites or to use simulated data to develop a workable optimization model. The former approach has not occurred while the latter is just beginning to appear in the literature.

Despite these data deficiencies, the conceptualizing of the analytical process of optimizing rangeland revegetation and use may be even more important than study results. That is, if the economic analysis is carefully thought through at the initiation of the study by both range managers and economists working together, the critical elements can be focused upon for decision-making and monitoring. The analytical methods and theory of economics can help structure this important process.

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The grass seedling: When is it established?

R.E. RIES AND T.J. SVEJCAR

Abstract

Adventitious roots of sufficient length and diameter must develop to assure that the photosynthetic surfaces receive sufficient water and nutrients before grass seedlings can be considered established. We evaluated development of crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] and blue grama [*Bouteloua gracilis* (H.B.K.) Lag.] seedlings in the field to decide when they were established. Blue grama and crested wheatgrass seedlings, under the environmental conditions of this study, were considered established 21 days after emergence. At this time, crested wheatgrass seedlings had 4 leaves, 2 adventitious roots penetrating to a depth of at least 80 mm into the soil, and 1 tiller per plant. Blue grama seedlings had about 6 leaves, 2 adventitious roots penetrating to a depth of at least 100 mm into the soil, and 2 tillers per plant. Most seedlings that reached this stage by the end of the first growing season overwintered and survived the following growing season and provided adequate stands for both species.

Key Words: blue grama, (*Bouteloua gracilis*), crested wheatgrass, (*Agropyron desertorum*), establishment, seedling development

It is often difficult to decide when establishment occurs following grass seeding. Seedling development occurs in 3 general stages including (1) heterotrophic stage, (2) transition stage, and (3) autotrophic stage (Whalley et al. 1966). It follows that a grass seedling should be completely autotrophic (not reliant on seed reserves) before being considered established.

Hyder et al. (1971) and Hyder (1974) compared morphologies of blue grama [*Bouteloua gracilis* (H.B.K.) Lag.] (type A "panicoid") and crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] (type B "festucoid") seedlings. Seedling morphology of the 2 grass species was vastly different. When both species were planted at 18 mm, crested wheatgrass initiated adventitious roots at the depth of planting and blue grama initiated roots at only 2 mm below the soil surface. Thus, adventitious roots of blue grama are exposed to the harsh environment associated with the soil surface, and chances or root survival are poor.

Successful establishment of grass seedlings requires formation of adventitious roots (Hyder et al. 1971). This requirement relates to the water conducting capacity of seminal compared to adventitious roots. Xylem cross-sectional area of the subcoleoptile internode (through which water from the seminal roots must flow) is generally not adequate to supply sufficient water to developing seedlings (Hyder et al. 1971, Wilson et al. 1976, Wilson and Briske 1978, Cornish 1982). For blue grama, the amount of seedling leaf area that the seminal root system could support reached a maximum 68 days after emergence. At this time, blue grama seedlings were vulnerable to atmospheric drought (Wilson and Briske 1978). The total cross-sectional area of xylem in a large adventitious root of blue grama was about 5 times greater than that of the subcoleoptile internode (Wilson et al. 1976). These authors also found that water uptake was 1 to 2 ml per day for blue grama seedlings with only a seminal root and 5 to 10 ml per day for seedlings with 1 large adventitious root (Wilson et al. 1976). Cornish (1982) also observed that the effective xylem radius of seminal roots restricts

water uptake and seedling growth for ryegrass (*Lolium perenne* L.) and phalaris (*Phalaris aquatica* L.). In further work, Cornish et al. (1984) found that delayed development of adventitious roots reduced transpiration of grass seedlings within 15 days of emergence and reduced leaf area and tiller development within 3 to 5 weeks. Most seedlings survived less than 4 months without adventitious roots, even when subsoil moisture was available to the seminal roots. Adventitious roots were able to support seedlings without seminal roots from about 20 days after sowing. Our objective was to evaluate the development of crested wheatgrass and blue grama seedlings in the field to decide when they could be considered established and document the above- and below-ground development of the grass seedlings at that time.

Study Area and Methods

This study was conducted at the Northern Great Plains Research Laboratory, Mandan, N.Dak., and is part of the study reported by Ries and Hofmann (1987). Soils of the study area are a Parshall fine sandy loam (coarse-loamy, mixed *Pachic Haploborolls*). This soil holds 19% soil water by weight at -0.03 MPa (field capacity) and 7% soil water by weight at -1.5 MPa (permanent wilting point). Plots were established on a tilled seedbed in a randomized, complete-block design with 2 replications. Crested wheatgrass and blue grama were seeded at 11 kg/ha of pure live seed on 21 June 1982. Crested wheatgrass was seeded with a drill with depth bands and packer wheels in 15-cm rows at an average 15-mm seeding depth. Blue grama was seeded by hand because its fluffiness did not allow it to flow evenly through the drill. It was seeded in 15-cm rows, raked to cover the seed, and rolled with a packer, at an average seeding depth of 10–12 mm.

Crested wheatgrass and blue grama seedlings for this study were subject to only natural weather conditions. Precipitation, air temperature, and free water evaporation were measured with standard U.S. Weather Bureau instruments and techniques. Weather data were averaged and reported weekly throughout the study except precipitation, which was recorded daily. Soil temperature at the surface ($n = 2$) and at seeding depth (13 mm) ($n = 4$) was recorded with ice bath calibrated maximum/minimum thermometers and averaged weekly. Soil water was monitored weekly by neutron probe to a depth of 2 m in 305 mm intervals. Gravimetric soil water samples were taken weekly from the soil surface to a depth of 76 mm in two 13 mm and two 25 mm increments.

Upon emergence, the development of numbers of leaves (main stem), adventitious roots, and tillers per each establishing crested wheatgrass and blue grama seedling was determined. Five seedlings/plot were dug from the soil each Friday, washed from the soil, and measured. Measurements recorded included actual seeding depth in the soil, depth from the soil surface to the point of adventitious root initiation, and depth adventitious roots had penetrated into the soil. Food reserves remaining in the caryopses were observationally evaluated by dissection to estimate the time seedlings could be considered autotrophic.

Weather and soil water data were plotted at the mid-point of each week to provide an evaluation of these parameters throughout the study period. Plant development data were plotted at the weekly harvest date to show sequential plant growth. Differences in seedling development between weekly harvest dates for each species were determined by analysis of variance using a protected

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Manuscript 6 May 1991.

Waller-Duncan test ($P \leq 0.05$) to separate significant mean differences.

Results and Discussion

Ries and Hoffman (1987) report 30 August 1982 densities of 26 and 606 plants/m² for crested wheatgrass and blue grama stands, respectively. The pattern and timing when water was received by the establishing stands appeared more important than amount of water received. The late seeding date (21 June 1982) and subsequent environmental conditions favored warm-season grass establishment.

Maximum soil surface temperatures were $20 \pm 2^\circ\text{C}$ warmer than maximum air temperatures. At the 13 mm soil depth, maximum soil temperature was about $10 \pm 1^\circ\text{C}$ lower than the soil surface temperature (Fig. 1). Minimum air and soil temperatures 13 mm in the soil were similar.

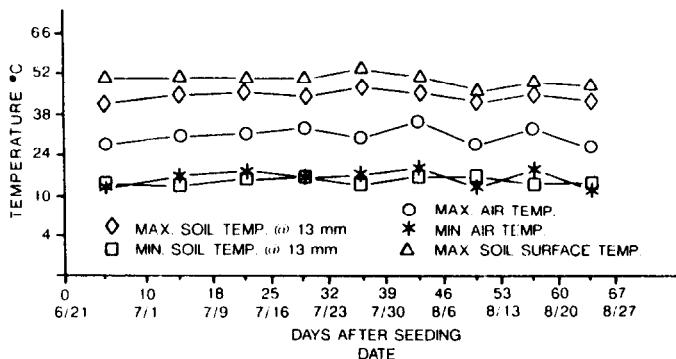


Fig. 1. Weekly average maximum and minimum air and soil temperatures during the summer of 1982 at Mandan, N.Dak.

The longest period without precipitation during the study was 9 days from 28 July through 5 August (Fig. 2). Precipitation received 8 July and 23 through 27 July was very effective because of low water demand as reflected in free water evaporation during these dates.

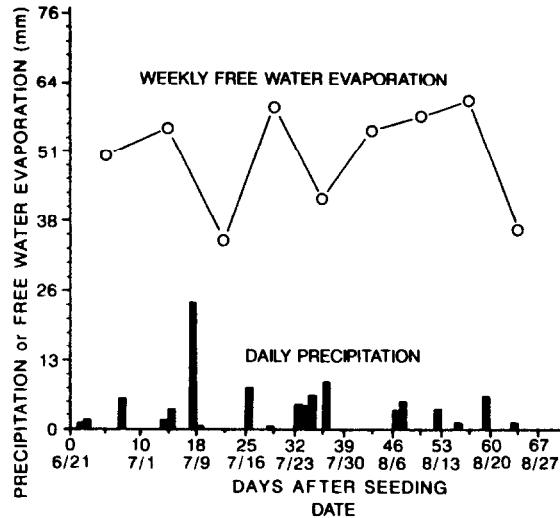


Fig. 2. Weekly average free water evaporation and daily precipitation during the summer of 1982 at Mandan, N.Dak.

Water from the rainfall event of 8 July increased the soil water at all levels in the soil (Fig. 3). The greatest increase in soil water occurred from the rainfall events during 23–27 July. The surface 13 mm of soil was drier than -1.5 MPa during 5 of the 9 sample periods.

Both species emerged during the same week, 25 days after seeding (Figs. 4 and 5). Emergence occurred after the 23 mm precipita-

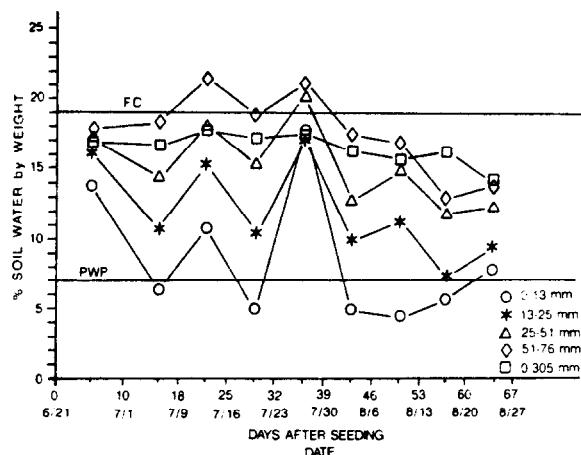


Fig. 3. Weekly average soil water during the summer of 1982 at Mandan, N.Dak. Soil is a Parshall fine sandy loam (coarse-loamy, mixed *Pachic Haploborolls*). (PWP = -1.5 MPa and FC = $-.03 \text{ MPa}$).

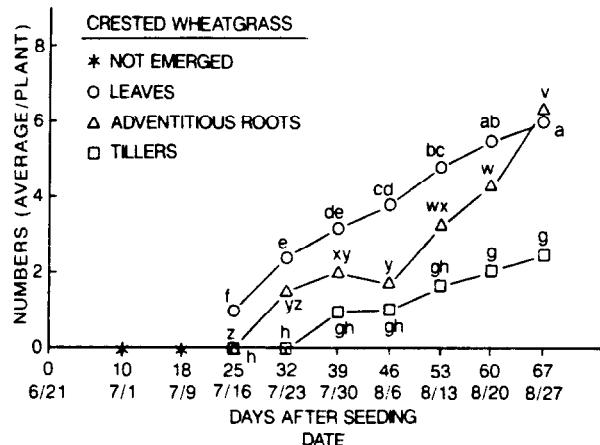


Fig. 4. Weekly number of leaves, adventitious roots, and tillers developed by crested wheatgrass seedlings during the summer of 1982. Points on the same line labeled with the same letter are not significantly different ($P \leq 0.05$).

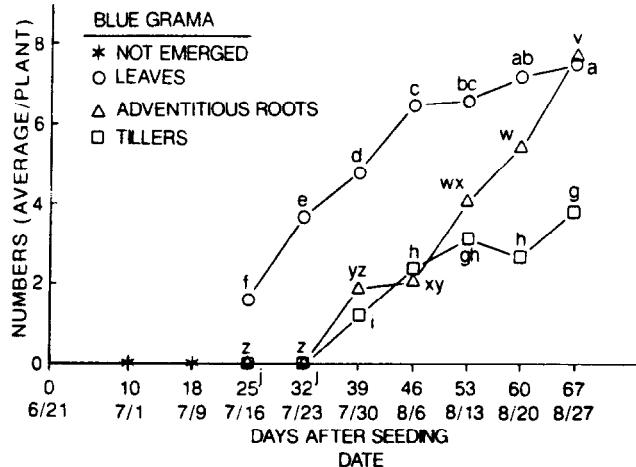


Fig. 5. Weekly number of leaves, adventitious roots, and tillers developed by blue grama seedlings during the summer of 1982. Points on the same line labeled with the same letter are not significantly different ($P \leq 0.05$).

tion event on 8 July (Fig. 2, Fig. 3). On 21 July, 17 and 39% of the pure live seed/m² had emerged for crested wheatgrass and blue grama, respectively. Leaf numbers for both species continually increased through the study.

Adventitious roots were observed on 20% of the crested wheatgrass seedlings during the week of 23 July, 7 days after emergence, while blue grama seedlings had no adventitious roots (Figs. 4 and 5). Adventitious roots were observed on 90% of the crested wheatgrass seedlings and 100% of the blue grama seedlings during the week of 30 July, 14 days after emergence (Figs. 4 and 5). The difference in time of adventitious root formation appears related to the type A (blue grama) vs. type B (crested wheatgrass) growth form. Crested wheatgrass initiated adventitious roots near planting depth (15 mm), where soil water was above -1.5 MPa from 17–23 July (Fig. 3). However, adventitious roots of blue grama were initiated only 5 mm below the soil surface where soil water was below -1.5 MPa during 17–23 July (Fig. 3). Initiation of adventitious roots by blue grama followed the precipitation event during 23–27 July (Fig. 2) that increased soil water (Fig. 3) in the 0–13 mm soil depth to above -1.5 MPa. This is consistent with the results reported by Hyder et al. (1971).

During the week of 31 July through 6 August mean maximum air and soil temperatures exceeded 35° C. On 6 August, sampled seedlings of crested wheatgrass (Fig. 4) and blue grama (Fig. 5) had not increased in number of adventitious roots since 30 July. On 6 August, adventitious roots were measured at soil depths greater than 80 mm for crested wheatgrass and 100 mm for blue grama. These depths were well into the zone of available soil water below 25 mm. Adventitious root numbers continued to increase after 6 August to 27 August when measurements ceased. Tiller formation was first observed for crested wheatgrass and blue grama during the week of 30 July, 14 days after emergence, and showed continual increase throughout the rest of the study (Figs. 4 and 5).

Adventitious root numbers and number of leaves increased proportionately until mid-August following adventitious root initiation (Figs. 4 and 5). After mid-August, the number of adventitious roots continued to increase at the same rate, but leaf numbers increased at a much slower rate. This gave essentially the same ratio of adventitious roots/leaves for both crested wheatgrass and blue grama (Fig. 6). Similarly, Svejcar (1990) found that the ratio of root length/leaf area of crested wheatgrass seedlings remained fairly constant during the first month of growth then increased during the second month.

Crested wheatgrass and blue grama seedlings in this study were considered established on 6 August (46 days after seeding and 21

days after emergence). Crested wheatgrass and blue grama seedlings in our study were autotrophic by 6 August because all seed food reserves were exhausted. At this time, crested wheatgrass seedlings had about 4 leaves, 2 adventitious roots, and 1 tiller per plant and blue grama seedlings had 6 leaves, 2 adventitious roots, and 2 tillers per plant. Adventitious roots had formed and had sufficient penetration into the soil to supply the available water (Fig. 3) to the photosynthesizing seedlings. The continuing increase in tiller and adventitious root numbers by the seedlings from 6 August throughout the rest of the study also supports the conclusion that establishment had occurred by 6 August (Figs. 4 and 5). Plant development can be rapid when environmental conditions are favorable. This is shown by the rapid increase in plants with adventitious roots from 23 July to 30 July and by the steep slope of the graph line for number of adventitious roots developed from 6 August to 27 August (Figs. 4 and 5). Observations of these stands the next September showed that most plants present in September 1982 survived the 1982–83 winter and 1983 growing season.

We believe that data presented in this paper support the theories in the literature concerning when grass seedlings are established. Under the environmental conditions of this study, seedlings of both species were considered established 46 days after seeding or 21 days after emergence. These data represent grass seedling development in response to a particular set of environmental conditions. The time required for emergence and leaf, adventitious root, and tiller development can be expected to be different under other sets of environmental conditions. In the future, seeding trials should include some assessment of when adventitious roots become established. Such information in conjunction with weather data will help in building a data base to better assess environmental impacts on seeding success.

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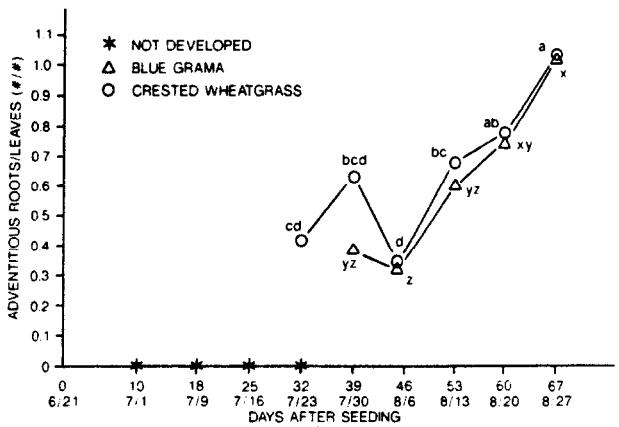


Fig. 6. Ratio of adventitious root number/leaf number for crested wheatgrass and blue grama seedlings during the summer of 1982. Points on same line labeled with the same letter are not significantly different ($P \leq 0.05$).

Leaf and whole plant transpiration in honey mesquite following severing of lateral roots

R.J. ANSLEY, P.W. JACOBY, AND R.A. HICKS

Abstract

This study examined water loss by fully grown honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) trees at 2 levels of resolution, the whole plant (canopy) and the individual leaf. Trees were manipulated by severing lateral roots during winter dormancy. Leaf transpiration and photosynthesis were measured in root-severed and unsevered (control) trees for 2 growing seasons following treatment. An empirical model which integrated leaf transpiration, whole plant leaf area, and influence of shading within the canopy on leaf transpiration was used to calculate daily water loss from individual trees. During the first growing season leaf abscission occurred on root-severed, but not control trees, in early July, resulting in a 50% reduction in whole plant leaf area. Following abscission, transpiration and photosynthesis of remaining leaves on root-severed trees were significantly greater than on control trees from July through September. Because of increased transpiration of remaining leaves on root-severed trees, daily water loss per tree was not significantly different between root-severed and similar-size control trees before or after leaf abscission. No differences in leaf or canopy transpiration were found between root-severed or unsevered honey mesquite during the second growing season. Daily water loss per tree ranged from 30 to 75 liters during the study. These responses illustrate that water loss from mesquite may be regulated by various combinations of stomatal control and adjustment of transpirational surface area.

Key Words: leaf area, photosynthesis, phreatophyte, stomatal conductance, water potential, water relations

Honey mesquite (*Prosopis glandulosa* Torr.) inhabit a variety of arid and semiarid environments in the southwestern USA and Mexico. In some regions, such as the Sonoran desert of California or the southern High Plains near Lubbock, Texas, mesquite have been described as drought-avoiding phreatophytes which utilize deep ground water via extensive taproots (Mooney et al. 1977, Thomas and Sosebee 1978, Levitt 1980). These phreatophytic mesquite also exhibit mechanisms of drought tolerance, including seasonally changing stomatal sensitivity and osmotic adjustment (Nilsen et al. 1981, Nilsen et al. 1983).

In regions where deep groundwater is minimal, mesquite often appear to be less than fully phreatophytic. These plants have developed an extensive system of lateral roots (Ludwig 1977, Heitschmidt et al. 1988) and respond rapidly to precipitation (Ansley et al. 1989). The degree to which lateral roots influence water

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Published with the approval of the director, Texas Agricultural Experiment Station as TA-25359. This research was funded in part by a grant from the Texas Water Development Board (Contract IAC 0940), Austin, Texas; the USDA Soil Conservation Service, Ft. Worth, Texas; and E. Paul and Helen Buck Waggoner Foundation, Vernon, Texas.

The authors wish to acknowledge Dave Price, Don Wilhoite, Tom Wright, and Steve Dowhower for assistance in data collection, Kathy Young for computer programming, and Fay Smith for typing the manuscript. We thank Rod Heitschmidt, Keith Owens, Bill Dugas, and David Briske for reviewing various drafts of this manuscript.

Manuscript accepted 26 January 1991.

relations of honey mesquite is not fully understood but may relate to the amount of available groundwater (Ansley et al. 1990).

Most studies of woody plant water relations in semiarid environments have been based on measurements of the individual leaf (Schulze and Hall 1982). Increasingly there is a need to relate whole plant responses to environmental changes (Pook 1985, Nilsen et al. 1987, Meinzer et al. 1988). It is not known whether leaf responses parallel whole plant responses under all conditions since microclimatic variation within the canopy influences leaf responses (Schulze et al. 1985, Caldwell et al. 1986, Gold and Caldwell 1989, Hinckley and Ceulemans 1989). This study was designed to determine water loss by honey mesquite at 2 levels of resolution, the whole plant and the individual leaf. The study complements earlier research which examined the influence of site on mesquite rooting strategies and water use (Ansley et al. 1990).

Materials and Methods

Study Area

Research was conducted on the Wagon Creek Spade Ranch located 16 km north of Throckmorton, Texas, in the Rolling Plains ecological region of north central Texas (99° 14'W, 33° 20'N; elevation 450 m). Soils on the study site are of the Nualde series (fine-silty, mixed, thermic family of typic Calcustolls). Average annual precipitation is 624 mm, which is distributed bimodally with peak rainfall periods in May and September. Average frost-free period is 220 days. Vegetation at the site is a mixture of mid-and shortgrasses with a 35% canopy cover overstory of mesquite which, to our knowledge, had never been manipulated by human control practices. Tree density is about 300–400 plants per ha. Mesquite growth form is erect and few-stemmed with the diameter of basal trunks on many of the plants in excess of 30 cm and heights in excess of 5 m. Dominant perennial herbaceous species are sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.), and Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.).

Treatment Installation

Six trees were selected for the study on the basis of uniformity of size and shape. Average height, canopy volume, and basal stem diameter (at 10 cm above ground) were 3.7 m, 25.8 m³, and 0.2 m, respectively. The trees occurred in open areas so that shading from adjacent larger trees was not a factor except at sunrise and sunset. In January 1986, a vertical trench 3 m deep was cut around each of 3 trees roughly 1 m beyond the lateral perimeter of each canopy. The soil wall on the tree side of the trench was wrapped with 2 layers of 6 mil plastic, and a fiberglass sheet was attached to the upper 0.5 m of the plastic barrier before refilling the trench. The fiberglass sheets extended 20 cm above the surface to prevent overland flow of water from entering or leaving the containerized area. These trees are referred to as "root-severed". The 3 trees with intact root systems are referred to as "controls". Root barriers were installed during winter dormancy (i.e., leaves were abscised), 3 months prior to mesquite budbreak. Precipitation was measured at the site with a tipping-bucket rain gauge.

Leaf Measurements

Leaf transpiration (E) and net photosynthesis (A) were measured monthly from April to September, 1986–1987, using a closed chamber system¹. Duration of each measurement was 40 seconds. Air flow rate in the chamber was varied to maintain chamber relative humidity (RH) at ambient RH levels (\pm percentage points). Measurements were made at 2-hour intervals during each sample day on 2 leaves on the sunlit aspect of each tree canopy. Leaves were selected from the canopy perimeter about 1.5 to 2 m above ground. Approximately 5–9 cm² (1 side) leaf area was enclosed in the chamber during each reading. Photosynthetically active radiation (PAR, 400 to 700 nm) was determined at the position on the canopy perimeter where E and A were measured using a quantum sensor² which was mounted to the leaf chamber. Sampling was conducted on clear or mostly clear days.

Predawn leaf petiole xylem water potential (predawn leaf Ψ) was measured on each E and A sample date. Two leaves were excised from the center of each canopy and measurements were made immediately with a Scholander pressure bomb (Turner 1981).

Whole Plant Leaf Area Determination

Whole plant leaf area (WPLA) was estimated for the control trees on 12 June and 23 July 1986 by clipping three 1.5-cm diameter (± 0.3 cm) branches (as subsamples) from each of 4 or 5 non-experimental trees growing near the control trees. All leaves were harvested and total leaf area per subsample was determined with an area meter. Leaf area per branch (1 leaf side) averaged 0.43 m² on 12 June and 0.40 m² on 23 July, representing a 7% reduction during the interval. Coefficient of variation in leaf area among trees and among subsamples on each date was less than 14 and 17%, respectively. WPLA of each control tree was determined by counting the number of 1.5-cm diameter branches which supported foliage, and multiplying that by the leaf area per branch that was determined from the nonexperimental trees.

WPLA of root-severed trees was determined in a similar manner as the control trees on 12 June 1986, when foliage appeared similar to that of adjacent nonexperimental trees. However, by 23 July, foliage declined on root-severed trees such that it was no longer visually comparable to that of nonexperimental trees. Thus, the technique employed to assess WPLA of control trees on this date was not considered valid for estimating WPLA of root-severed trees. Therefore, on 23 July foliage reduction of root-severed trees was visually estimated by 6 individuals after comparing growth to that of adjacent nonexperimental trees. Average percent reduction in foliage on root-severed trees when compared to adjacent trees on this date was 42.8 (s.e. = 5.3, n = 3). To estimate foliage reduction on root-severed trees from 12 June to 23 July, an additional 7% was added to the 42.8 value to account for the decline in foliage on control trees during this interval (7% was derived from the 0.43 to 0.40 m² decline in leaf area per branch).

In 1987, WPLA was estimated monthly from mid-May to mid-September using a digital image analysis procedure based on photographs of the trees (Ansley et al. 1988). Side-view black and white photographs of entire canopies of experimental and non-experimental trees were obtained from fixed points 20 m from each tree and using a 300-mm telephoto lens. Within 3–4 days after each photography date, nonexperimental trees were completely harvested. Total leaf area per tree was determined by obtaining total leaf weight (oven dry at 80° C) and establishing weight:area regressions (using subsamples of the total leaf mass and an area meter). Tree images were outlined with a marker and area within the outline was

determined using a tablet digitizer and computer software³. Regressions between digital values of the images and WPLA of harvested trees were established for each sample date (Table 1) and used to predict WPLA of the experimental trees. WPLA values obtained using the photographic method did not differ significantly ($P < 0.05$) from those obtained by branch harvesting method,

Table 1. Regression equations between leaf area and digital values of side-view images of trees harvested on several dates in 1987.

Date	No. trees harvested	Regression equation	r ²	F
11 May/19 Sept. ¹	6	$Y = 3.60 x - 1.69^2$.98	190** ³
11 June	6	$Y = 3.15 x - 1.80$.95	84**
10 July	6	$Y = 2.55 x - 0.25$.84	21*
07 August	6	$Y = 2.30 x - 0.31$.76	13*

¹Dates with similar regressions were pooled.

²Y = Whole plant leaf area (one leaf side; m²); X = digital values of canopy images (units are m² side-view area of canopy).

* = significant at $P \leq 0.05$; ** = Significant at $P \leq 0.01$.

as described earlier, when nonexperimental trees were used to compare the 2 methods in 1987.

Whole Plant Transpiration

A multilayer model was developed to estimate daily whole plant transpiration (WPE). Estimates were based on an integration of E , WPLA, and a series of empirically derived coefficients, termed transpiration coefficients (TC), designed to account for variation of E as influenced by shading within layers of the canopy (Schulze et al. 1982, Landsberg and McMurtrie 1984, Caldwell et al. 1986, Raupach and Finnigan 1988). A "day" in the model was defined as the 10-hour period from 1 to 11 hours post sunrise (HPS) in 1986 and 2 to 12 HPS in 1987. Each day in the model was segmented into five 2-hour intervals (i) so that:

$$WPE = \sum E_{2ij} \quad (1)$$

where,

WPE = Daily whole plant transpiration (kmol H₂O tree⁻¹ day⁻¹), and

E_{2ij} = Two-hour whole plant transpiration (mol H₂O tree⁻¹ 2 hr⁻¹) at 2-hour interval i (for i=1..n, 1=1–3HPS; 2=3–5 HPS, 3=5–7 HPS, 4=7–9 HPS, 5=9–11 HPS), on date j (add 1 to HPS values for 1987).

To determine TC values, once during spring and again in mid-summer of both years (4 sample periods total), 1 control tree was selected for intensive sampling in which E was measured within 4 diurnally changing shade layers within the canopy. Each layer was visually estimated to contain 25% of WPLA. Boundaries of each layer were oriented perpendicularly to solar angle during each sample period. Six measurements of E and PAR were made per layer during each sample period. Sample periods coincided with pre-defined 2-hour intervals. TC's within the 3 shaded layers (L2–L4) were expressed relative to the most sunlit layer (L1) so that:

$$TC_s = E_s / E_0 \quad (2)$$

where,

TC_s = Transpiration Coefficient at shade layer s,

E_s = Leaf transpiration (mmol m⁻² s⁻¹) at shade layer s, and

E_0 = Leaf transpiration (mmol m⁻² s⁻¹) at the most sunlit layer, L1.

To determine the influence of canopy shading on PAR, radiation coefficients (RC) were determined in a similar manner as transpiration coefficients, so that:

¹LICOR Model LI-6000, Lambda Inst. Inc., Lincoln, NE.

²LICOR Model LI-190S-1, Lambda Inst. Inc., Lincoln, NE.

³Sigma-Scan software, Jandel Scientific, Corte Madera, CA.

where,

$$\begin{aligned} RC_s &= \text{Radiation Coefficient at shade layer } s, \\ PAR_s &= \text{PAR (uE m}^{-2} \text{s}^{-1}\text{) at shade layer } s, \text{ and} \\ PAR_0 &= \text{PAR (uE m}^{-2} \text{s}^{-1}\text{) at the most sunlit layer, L1} \end{aligned}$$

When averaged over all 4 sample periods, E was reduced by 17, 26, and 38% (i.e., TC = 0.83, 0.74, and 0.62) in shade layers L2, L3, and L4, respectively. PAR was reduced by 47, 68, and 82% (i.e., RC = 0.53, 0.32, and 0.18) in shade layers L2, L3, and L4, respectively.

Values for E_{2ij} were determined by integrating E and TC values so that for i=1...5 on date j,

$$E_2 = [\sum (E * TC_s)] * (WPLA * .25), \quad (4)$$

where,

E = Leaf transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$) on the sun-exposed aspect of the canopy,

TC_s = Transpiration coefficient within shade layer s (for s=1...n, 1=L1, 2=L2, 3=L3, and 4=L4), and

WPLA = Whole plant leaf area (m^2 ; includes both leaf sides).

Statistical Analysis

A one-way completely randomized analysis of variance (AOV) was used to evaluate 2 levels of root treatment (severing and control) as sources of variation of E during a particular HPS and date. A repeated measures AOV was used to evaluate effects of root treatment and date as sources of variation of average daily E, average daily A, predawn leaf Ψ , WPLA, and WPE (Steel and Torrie 1980). Prior to each analysis, within-tree subsamples were pooled so that n=3 (trees) per root treatment. Average daily E and A were determined by averaging E or A values from 1-11 HPS (1986) and 2-12 HPS (1987).

Results

Precipitation

Monthly precipitation was much less from October to March, prior to the 1986 mesquite growing season, than prior to the 1987 growing season, when precipitation was above normal (Fig. 1). During the mesquite growing season, precipitation was above normal in April and May 1986 and well above amounts which occurred during the same 2 months in 1987. Precipitation was above normal in June and near or below normal from July through September in both years.

Mesquite Phenology

Mesquite budbreak occurred on root-severed and control trees in mid-March 1986. Leaves were fully expanded by the last week in April. In 1987, budbreak did not occur until mid-April, and leaves were not fully expanded until mid-May on trees in both treatments. Leaf abscission from frost occurred on all trees in mid-November during both years.

Leaf Transpiration

Transpiration of sun-exposed leaves (E) on control trees displayed maximum values at 7 hours post sunrise (HPS) in April and September, and earlier in the day (1 or 3 HPS) from 21 May through 12 August 1986 (Fig. 2). E was similar in root-severed and control trees from April through June 1986, but was significantly greater in root-severed trees than control trees at most HPS from July through September. E was similar in both treatments during 1987.

Average daily transpiration of sun-exposed leaves (average daily E) was similar between treatments from April through June 1986, but was significantly greater (range of 38 to 53%) in root-severed than control trees from July through September (Fig. 3 a). There

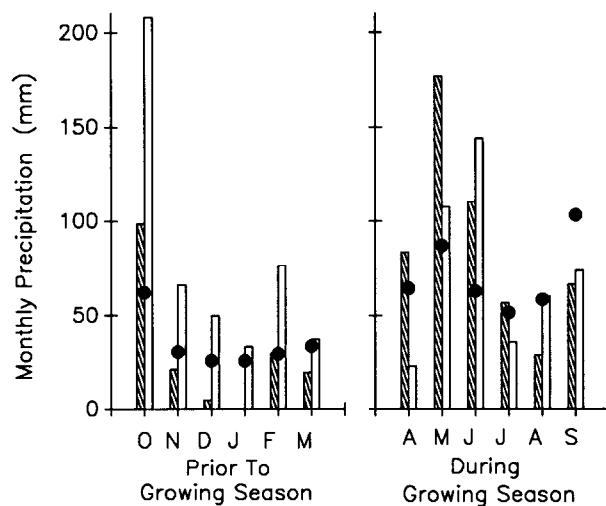


Fig. 1. Monthly precipitation totals at the study area near Throckmorton, Texas, during months prior to and during the mesquite growing season. Hatched bars: prior to 1986 growing season (left) and during the 1986 growing season (right). Open bars: prior to 1987 growing season (left) and during the 1987 growing season (right). Solid circles indicate 30 year average for each month obtained from National Oceanic and Atmospheric Administration (NOAA) records at a station 15 km from the research site.

were no significant differences in average daily E between treatments in 1987 (Fig. 3 b). Average daily E of control trees tended to be greater on comparable dates in 1986 than 1987 (Fig. 3 a-b).

Whole Plant Leaf Area

On 12 June 1986, whole plant leaf area (WPLA) was similar between treatments (Fig. 3 c). WPLA decreased slightly (7%) in control trees from 12 June to 23 July 1986. During the same interval, WPLA decreased by 50% in root-severed trees to levels which were significantly lower than those of control trees. The abscission of leaves on root-severed trees occurred very rapidly within a 4 to 6 day interval during the first week of July. Root-severed trees appeared to replace little leaf area during the rest of the 1986 growing season, although this was not measured.

During 1987, WPLA decreased in both treatments from 11 May to 7 August. The decrease was slightly more in root-severed than control trees. However, no significant differences in WPLA were found between treatments in 1987, (Fig. 3 d).

Daily Whole Plant Transpiration

Daily whole plant transpiration (WPE) was similar between treatments on all sample dates in 1986 (Fig. 3 e). From April to June 1986, similarities in WPE between treatments occurred because of similar average daily E and WPLA values between treatments (Fig. 3 a,c). Following differential reduction in WPLA between root-severed and control trees in early July 1986, E of remaining leaves on root-severed trees increased relative to control trees, producing similar WPE values between treatments from July to September 1986, although WPE was slightly, but not significantly, lower in root-severed than control trees toward the end of the 1986 growing season (Fig. 3 a,c,e). WPE was similar in root-severed and control trees on all dates in 1987 (Fig. 3 f).

Predawn Ψ and Photosynthesis

Predawn leaf Ψ was significantly less in root-severed than control trees in June 1986 (Fig. 4). Following a decline in both treatments during July, predawn leaf Ψ was significantly greater in root-severed than control trees in August 1986. There were no

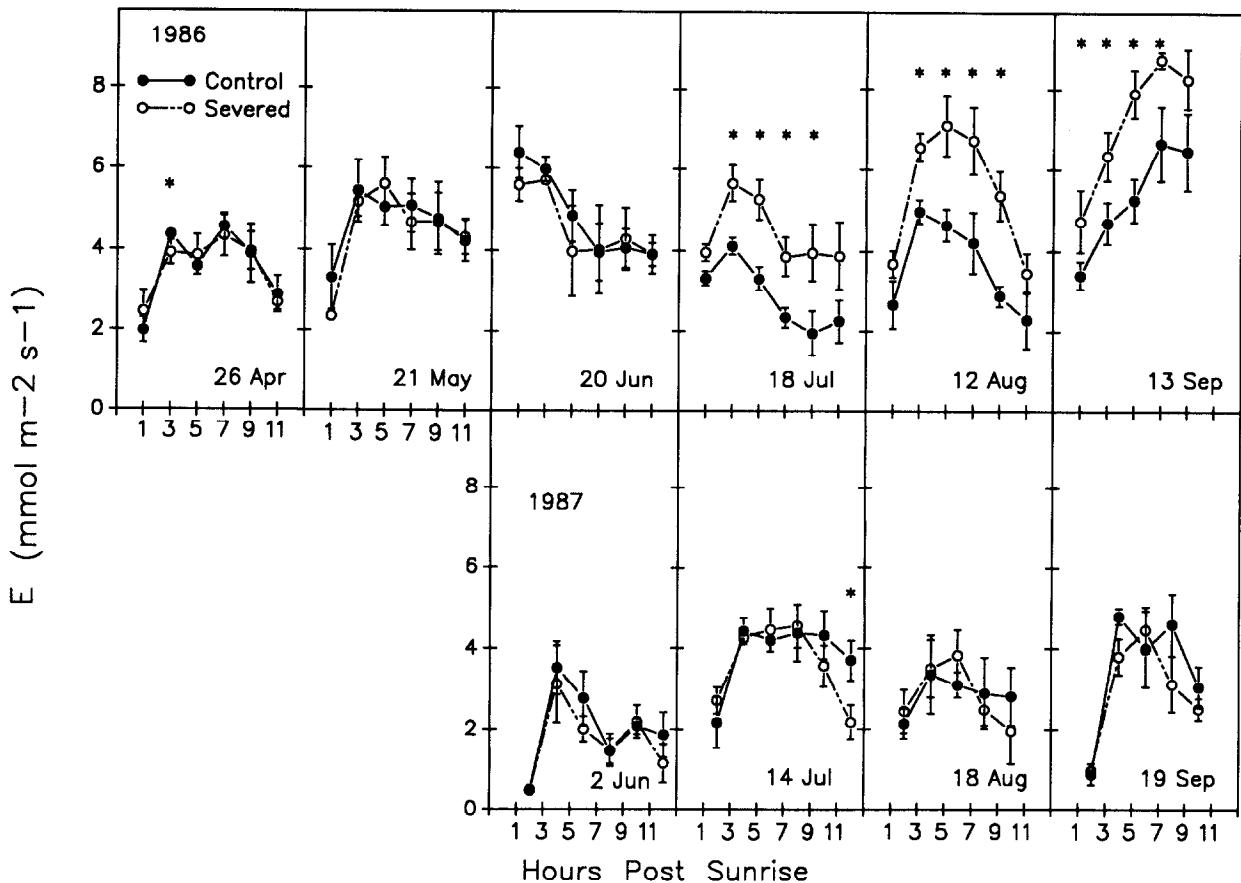


Fig. 2. Diurnal leaf transpiration (E) on control and root-severed mesquite on several dates in 1986 and 1987. An asterisk identifies a significant difference between the root treatments at a particular hour post sunrise ($P \leq 0.05$). Vertical bars indicate ± 1 standard error.

significant differences in predawn leaf Ψ between treatments in 1987.

Average daily leaf photosynthesis (average daily A) was similar between treatments in May and June 1986, but was significantly greater (range of 34 to 48%) in root-severed than control trees from July through September (Fig. 4). Average daily A was similar between treatments in 1987 except in early June and September when it was slightly (but not significantly) lower in root-severed than control trees.

Discussion

Estimation of Whole Plant Transpiration

Results from this study indicated mesquite water loss ranged from 1.7 to 4.2 kmol tree $^{-1}$ day $^{-1}$, or 30 to 75 liters tree $^{-1}$ day $^{-1}$. In his book, Larcher (1975) noted that the average loss of water per day of a birch (*Betula* spp.) tree on a sunny summer day was about 100 liters. Schultze et al. (1985) estimated daily transpiration of coniferous trees *Picea abies* and *Larix* spp. to be 75 and 63 liters per day, as measured by a discontinuous gas exchange porometer and extrapolated over total canopy area. Water use by phreatophytic honey mesquite in the Sonoran desert of California was estimated at 12,000 liters per year (Nilsen et al. 1983, Jarrell et al. 1990), which we estimated to be about 56 liters per day, based on an April–October growing season (214 days). In summary, estimates of WPE in our study appear to be compatible with other studies, although our maximum WPE values were higher than that previously reported for mesquite.

Leaf and Whole Plant Responses

The data suggest that moisture stress in root-severed mesquite was no greater than in control trees during the first part of the 1986

growing season, April through mid-June, when precipitation was well above normal. The onset of stress in root-severed trees appeared to be very acute, occurring in late June when predawn leaf Ψ was significantly lower in these trees than in control trees. The response to alleviate stress was also rapid. All defoliation in root-severed trees occurred within about 4–6 days in early July, about 2 weeks after differential stress between treatments was first detected.

Leaf abscission during the growing season is generally the result of moisture stress (Kozlowski 1976). Abscission in root-severed mesquite was likely an adjustment to compensate for an imbalance between transpirational surface area and ability of remaining unsevered roots to provide sufficient water. Kaufmann and Fiscus (1985) discussed the hypothesis that plants attempt to maintain a balance between leaf area and absorbing area of fine roots. However, unlike predawn leaf Ψ , other leaf variables we measured, such as E and A , were not different between control and root-severed trees prior to abscission in root-severed trees. Thus, leaf responses did not clearly indicate that root-severed trees were stressed prior to leaf shedding.

While many studies have demonstrated that stomata respond directly to stimuli from the microenvironment near the leaf (Cowan 1977, Farquhar and Sharkey 1982, Spence et al. 1983), reduction in leaf area, as found in root-severed but not unsevered mesquite in 1986, suggests the presence of a root-system based regulation of water loss which outweighed responses of individual leaves to leaf microenvironment. Research by others has demonstrated that root systems of drought-stressed plants signal leaves via abscisic acid (ABA) which is produced in the roots and transported to the leaves where it may influence either stomatal closure or abscission (Cornish and Zeevaart 1985, Zhang et al. 1987). This

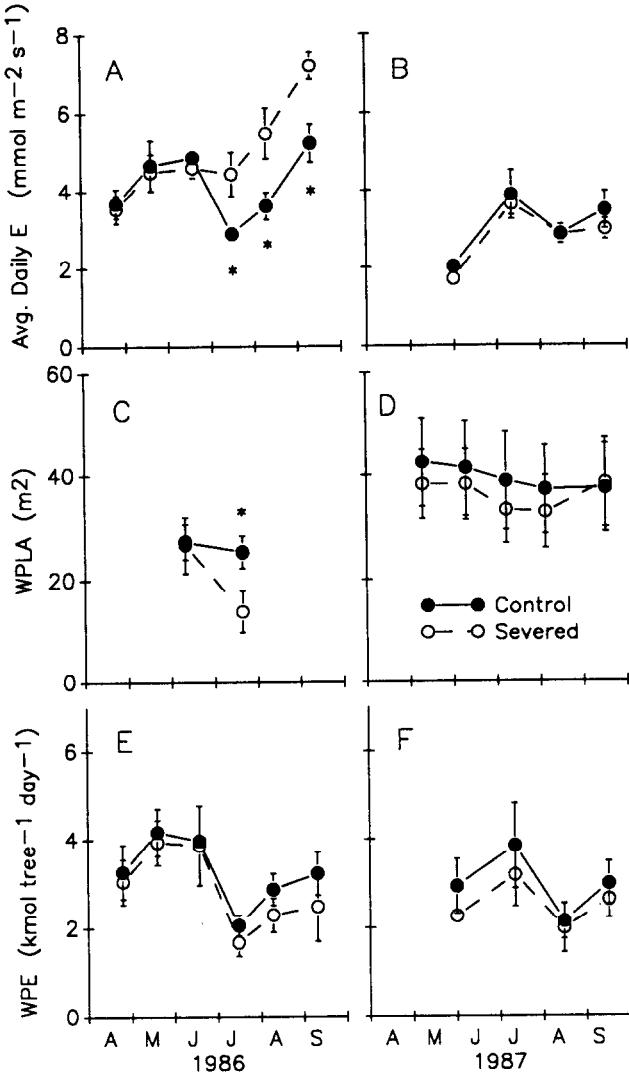


Fig. 3. Average daily leaf transpiration (Average daily E, top), whole plant leaf area (middle), and daily whole plant transpiration (WPE, bottom) of control (solid line) and root-severed (dashed line) mesquite at Spade Wagon Creek. Values for WPLA and WPE were determined using both leaf sides. An asterisk indicates a significant difference ($P < 0.05$) between treatments on a particular date. Vertical bars indicate ± 1 standard error.

process may have caused leaf abscission in root-severed mesquite, although measurements of ABA were not conducted. The rapidity of abscission in mesquite (occurring within 4–6 days) is in agreement with the ABA studies which indicated that following root sensation of soil drought, ABA production in roots, as well as responses of leaves to root-produced ABA, were rapid.

Following abscission, increases in A and E of remaining leaves on root-severed mesquite relative to control trees were similar to responses of remaining leaves of some grasses (Painter and Detling 1981, McNaughton 1983, Nowak and Caldwell 1984) and trees (Heichel and Turner 1983) following partial defoliation. Black and Mack (1986) found an increase in E of remaining leaves on big sagebrush (*Artemisia tridentata*) following leaf abscission during summer drought. The increases in A and E found in these studies may have been necessary to facilitate compensatory leaf growth. Detling et al. (1979) reported an increase in the proportion of current photosynthate allocated to synthesis of new leaves following defoliation of blue grama (*Bouteloua gracilis*). Conversely, McNaughton (1983) suggested that defoliation may conserve soil water and thereby improve water status of remaining leaves.

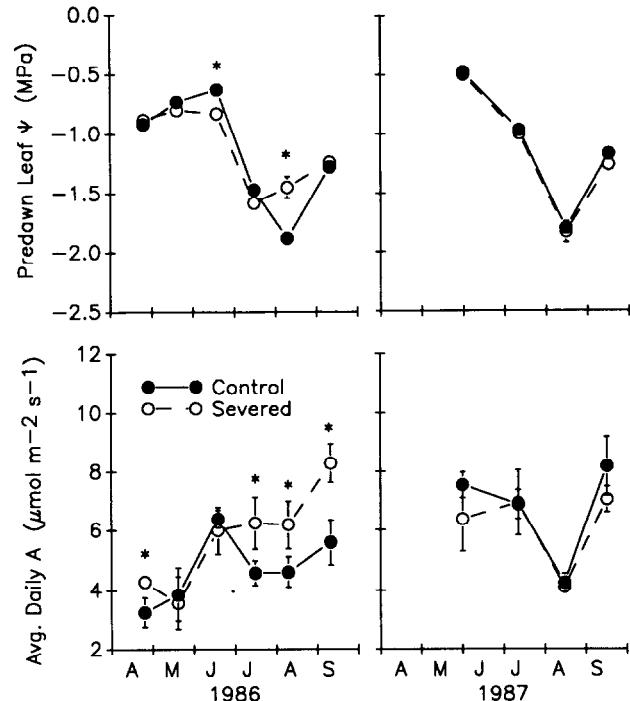


Fig. 4. Predawn leaf water potential (top) and average daily leaf photosynthesis (average daily A, bottom) of control (solid line) and root-severed (dashed line) trees at Spade Wagon Creek. An asterisk indicates a significant difference ($P < 0.05$) between treatments on a particular date. Vertical bars are ± 1 standard error.

Post-abscission responses by root-severed mesquite were similar to those of red oak (*Quercus rubra*) and red maple (*Acer rubrum*) in a study reported by Heichel and Turner (1983). These species replaced little leaf area following 50% defoliation, although remaining leaves had 54 and 75% increases in A, and 46 and 36% increases in stomatal conductance, respectively, when compared to undefoliated control trees.

Since we did not observe compensatory leaf growth on defoliated mesquite, the increased A and E following abscission may have been necessary for compensatory root growth. Several studies have reported increased A and E in leaves, as well as growth of new roots, following root pruning (Geisler and Ferree 1984, Ruff et al. 1987, Crombie et al. 1987). Richards and Rowe (1977) observed a redistribution of assimilates to roots following root pruning of peach (*Prunus persica*).

It is not known, if, when, or to what degree compensatory root growth occurred in mesquite. However, the absence of differential abscission between treatments in 1987 suggests root-severed trees had adjusted to the containerized environment by the second year of the study. These results are similar to those found by Ansley et al. (1990) in which reduction of stomatal conductance in root-severed trees was found during the first year following lateral root severing but not during the second growing season. These studies illustrate a previously undocumented aspect of the tremendous plasticity of this invasive woody plant in the way of root system recovery following severe manipulation.

Lateral Root Dependence

Honey mesquite exhibit phreatophytic behavior in some regions, such as the Sonoran desert of southern California (Mooney et al. 1977, Nilsen et al. 1984). This is attributed to the plant's ability to acquire an abundant supply of water via a deep taproot (Phillips 1963, Jarrell et al. 1990). Aboveground responses associated with this behavior include a relatively constant seasonal pattern of leaf

transpiration and maintenance of maximum canopy leaf area (Nilsen et al. 1983). Under these circumstances, regulation of water loss by the plant may be secondarily important to water acquisition. In contrast, results from our study, and from a similar study by Ansley et al. (1990), imply that on certain sites mesquite may not have a well-developed taproot and may depend primarily on lateral roots for water acquisition, thereby magnifying the importance of canopy regulation of water loss.

Results from the current study and the study by Ansley et al. (1990), which was conducted on 2 sites 60 km from the current study area, illustrate a variety of responses of mesquite to severing of lateral roots. On 1 site reported by Ansley et al. (1990), stomatal conductance was significantly reduced in root-severed trees when compared to unsevered control trees. On the second site reported in their study, stomatal conductance was only slightly reduced in root-severed trees. Plant leaf area was not affected by lateral root severing on either site. In the present study, leaf abscission in response to later root severing indicated an extreme dependence on lateral roots. The importance of these roots is elevated further when considering that precipitation was well above normal during April through June 1986 (Fig. 1), yet abscission still occurred. These studies suggest that as dependence on lateral roots increased among sites, response to severing of these roots proceeded from a slight reduction in stomatal conductance, to substantial stomatal regulation of water loss, and finally leaf abscission. Degree of dependence on lateral roots may relate to subsoil characteristics on a particular site (Ansley et al. 1990). Results from these studies indicate that strategies for regulation of water loss by this invasive woody plant vary with site and may involve a combination of stomatal control and adjustment of transpirational surface area.

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Use of ornamental lilac and honeysuckle phenophases as indicators of rangeland grasshopper development

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Abstract

Comparisons were made between phenological phase dates of 2 common ornamental shrubs, purple common lilac (*Syringa vulgaris* L.) and Zabeli honeysuckle (*Lonicera krolkowii* Stapf, var. *Zabelii* (Rehd. Rehder)), and rangeland grasshopper (composite of 6 common species) development for 3 years at 9 sites throughout Montana. Results indicated that spring hatch (75% instar 1) occurred about 10 days after the begin bloom phase of purple common lilac. Peak occurrence of grasshoppers for instar 2 coincided, on average, with the end bloom phase of Zabeli honeysuckle, whereas peak instar 3 occurred about 10 days later. On average, peak instar 4 preceded the first red berry phase of Zabeli honeysuckle by about 8 days, and 75% adult stage occurred about 14 days after red berries first appeared. Our results provide rangeland managers and ranchers with a simple method for the improved timing of assessment and control of rangeland grasshoppers.

Key Words: IPM, phenology models, rangeland insects, *Lonicera krolkowii*, *Syringa vulgaris*, grasshoppers, *Acrididae*, geostatistics

The sequence of activities involved in rangeland grasshopper pest management are generally triggered by the presence of specific life stages in the field. Grasshoppers commonly have 5 nymphal stages (instars 1–5) followed by the adult stage. Onsager (1987a, 1987b) states that the best time to evaluate rangeland grasshopper densities is at "peak instar 3". Peak instar 3 refers to the point in time when we expect to have the highest proportion of instar 3 individuals for a given site and year. By assessing densities of grasshopper communities at peak instar 3, resource managers still have time to prepare for and apply biological or chemical control agents at the appropriate times (for example, at peak instars 4 and 5 or 25% adult).

A statistical model has been developed that describes insect

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The authors wish to thank J. Holmes, K. Curtiss, T. Engle, D. Gillis, and V. Hagestad for technical assistance. The reviews and comments of early drafts of this manuscript by Dr. Stephen A. Woods, Dr. Jeffrey A. Lockwood, and Dr. Jerome A. Onsager are sincerely appreciated. Thanks also go to S. Osborne and P. Rowsey for manuscript preparation.

This work was supported in part by a cooperative agreement with the Grasshopper IPM Demonstration Program USDA-APHIS-PPQ, Boise, Idaho.

Manuscript accepted 31 January 1991.

phenology as a function of accumulated heat or degree days (Dennis et al. 1986, Dennis and Kemp 1988). The model (Dennis et al. 1986) and related statistical inferences (Dennis and Kemp 1988) can be used to develop estimates of the average date of occurrence for the different developmental phases of rangeland grasshoppers. However, resource managers are frequently not able to obtain the data (daily maximum and minimum temperatures, and grasshopper development) required for computing parameter estimates for the model. Therefore, it is important to evaluate the relationships between rangeland grasshopper phenology (using methods of Dennis et al. 1986 and Dennis and Kemp 1988) and other indicator variables such as plant phenophases.

Recognition that the annual progression of plant development has important implications to rangeland management is not new. Plant phenophases have been used to determine range readiness, to select for the timing of brush control (Hyder and Sneva 1955), and to describe climatic patterns (Caprio 1966). Developmental stages of indicator plants have also been associated with insects. For example, Hewitt (1979) found a loose association between later instar rangeland grasshoppers and phenological stages of 3 grass species at Roundup, Mont., over a 3-year period. Other studies of rangeland grasshopper populations (Hewitt 1980) have suggested a possible link between 14 rangeland forb species and an unidentified complex of grasshopper species during a 2-year study at 2 sites in Montana. However, because of the variability found in plant phenology that resulted primarily from precipitation patterns, Hewitt (1979, 1980) suggested that a combination of plants would be necessary to estimate grasshopper phenology.

Kemp (1987) suggested a link between peak instar 3 of rangeland grasshoppers, the end bloom phase of Zabeli honeysuckle (*Lonicera krolkowii* Stapf, var. *Zabelii* (Rehd. Rehder)), and begin bloom phase of purple common lilac (*Syringa vulgaris* L.) based on data collected during 2 years at 1 site. Use of ornamentals grown Zabeli honeysuckle and purple common lilac as phenological indicators for grasshoppers has several advantages over native range plants (Hewitt 1979, 1980). In the western United States, for example, there exists a network of purple common lilac and Zabeli honeysuckle observers who utilize standard methods in recording plant phase observations each year (Caprio 1966, Caprio et al. 1970). These plants are also extensively grown in home gardens throughout Montana. Further, because observers monitor the

same plants each year and provide standardized care (for example, planting, watering, pruning, etc. (Caprio et al. 1970)), the progression of phenological stages of purple common lilac and Zabeli honeysuckle is a good indicator of total heat input at a given site (Caprio 1967, 1974). Attempts to relate plant development to the seasonal development of ectotherms such as grasshoppers are likely to be most successful where plant phenology is driven primarily by heat and is not influenced by both heat and precipitation, as was the case for native plants used in previous studies (Hewitt 1979, 1980).

The objective of this study was to examine the relationships between seasonal phenology of purple common lilac, Zabeli honeysuckle, and rangeland grasshoppers in Montana in order to provide resource managers a simple method for determining when grasshopper pest management decisions should be made. At present, such decisions require on-site sampling by trained individuals because no predictive development models exist that can be used by land managers.

Methods

Indicator Plant Phenology Data

Phenological observations on both purple common lilac and Zabeli honeysuckle were made during 1986–1988 at about 40 locations throughout Montana, eastern Idaho, and northern Wyoming. These plant phenological observations are part of an ongoing study of large scale spatial patterns of plant phenology throughout the western United States (Hopp 1974). Within this network, observers follow standard procedures for planting, maintenance, and observation for both purple common lilac and Zabeli honeysuckle (Caprio et al. 1970). For each year, a relationship was developed between elevation (Table 1) and each of 3 selected plant

Table 1. Elevation correction coefficients (days/30.5m) used to adjust the phenology dates for the interpolation process.

	1986	1987	1988
Begin bloom purple common lilac	0.91	0.68	0.95
End bloom Zabeli honeysuckle	— ¹	— ²	1.03
First red berry	1.04	— ³	1.18
95% red berry	0.90	0.84	— ⁴

¹Kriging was not successful. Mean number of days from begin bloom to end bloom was calculated (23.7 days) and added to the interpolated begin bloom dates on a per grid location basis (cell).

²There was not a significant coefficient for elevation correction. However, a significant regression (Interval (days) = $-4965.0 + 212.78 * \text{latitude} - 2.2639 * \text{latitude}^2$) was found to estimate the number of days from begin bloom to end bloom. This interval (days) was calculated on a per cell basis and added to the interpolated dates for begin bloom.

³There was not a significant coefficient for elevation correction. However, a significant regression (Interval (days) = $55.43 + -0.2693 * \text{latitude}$) was found to estimate the number of days from first red berry to 95% red berry. This interval (days) was calculated on a per cell basis and subtracted from the interpolated dates for 95% red berry.

⁴There was not a significant coefficient for elevation correction. The interval from first red berry to 95% red berry was calculated for each observed data point. Kriging was used to interpolate these intervals. These interpolated intervals were added to the interpolated dates for first red berry.

development stages (begin bloom phase of purple common lilac¹, end bloom phase of Zabeli honeysuckle², and first red berry phase of Zabeli honeysuckle³). These relationships were used with an interpolation method known as block kriging to produce a normalized map for each development phase at an elevation of 1,216 m (Englund and Sparks 1988, Robertson 1987) except where noted in Table 1. These maps were then used together with the derived relationship with elevation to estimate the Julian date (by year) for each plant phase within 12.87 km² cells throughout Montana. If the elevation of a cell differed by more than 30.5 m from the actual elevation of a grasshopper monitoring site, an additional lapse rate adjustment was made on the estimated event date of a

¹Begin bloom phase of purple common lilac is the date when the first flower is fully open (Caprio et al. 1974).

²End bloom phase of Zabeli honeysuckle is the date when nearly all (at least 95%) of all flowers have withered or dried up (Caprio et al. 1974).

³First red berry phase of Zabeli honeysuckle is the date when the first berry has turned to a definite red color (Caprio et al. 1974).

specific plant phase. The elevation assigned to a cell was an average of the highest and lowest elevation within a cell. Adjustments made with this second correction factor altered estimates by no more than (+ or -) 3 days.

Grasshopper Data

Rangeland grasshopper species composition was monitored from 1986–1988 at 9 selected sites throughout Montana. We located sites over a range of long-term plant phenological zones (see, Kemp [1987] Fig. 24.6). All but one of the sites were located within 3.2 km of a local airport and functioning National Oceanic and Atmospheric Administration (NOAA) weather station. On-site temperatures were recorded at the Three Forks site because there was no nearby NOAA station. Weather permitting, weekly samples were collected at each of the sites during the intervals shown in Table 2. Species composition and phenological stages for grasshoppers were determined via weekly sweep net collections at each site.

Table 2. Location, elevation, and recording dates for each of 9 sites monitored for rangeland grasshoppers densities, Montana.

Location	Elev.	First and last collection dates		
		1986	1987	1988
Glasgow	695m	5/27–9/24	4/16–9/22	4/19–9/14
Havre	790m	5/21–9/24	4/16–9/21	4/18–9/15
Miles City	799m	5/21–9/23	4/15–9/22	4/19–9/13
Jordan	802m	5/30–9/24	4/15–9/22	4/19–9/14
Fort Benton	875m	5/20–9/24	4/16–9/21	4/18–9/15
Broadus	921m	5/21–9/23	4/15–9/23	4/20–9/13
Billings	1,049m	5/19–9/23	4/14–9/23	4/21–9/13
Great Falls	1,125m	5/28–9/24	4/17–9/21	4/18–9/15
Three Forks (DCP)	1,348m	5/2–9/12	4/7–10/1	5/3–9/23

Prior to analyses, 6 common rangeland grasshopper species were selected as being representative of the assemblage of species at each site. These were *Ageneotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Aulocara ellioti* (Thomas), *Melanoplus infantilis* Scudder, *M. packardii* Scudder, and *M. sanguinipes* (F.). Kemp and Onsager (1986) used this assemblage to make standardized comparisons between rangeland grasshopper phenological patterns in 2 different years at Roundup, Mont. While we recognize that the rangeland grasshopper assemblages vary spatially (Kemp et al. 1990a) and temporally, we decided that it was important to restrict comparisons to common species of major economic importance that had similar springtime phenological patterns.

The association between the 3 selected plant development stages and rangeland grasshopper phenology was investigated in several steps. First, as noted above, the Julian date of each plant phenological stage for each grasshopper sample site was estimated based on its elevation, latitude, and longitude (Tables 1 and 2). Second, the methods of Dennis et al. (1986) were used to generate parameters for a model that describes rangeland grasshopper phenology as a function of accumulated heat (Kemp and Onsager 1986, Kemp 1987). Estimates of accumulated heat at each site and year (degree days, 17.8° C base) were computed with a sine wave method of Allen (1976) from maximum and minimum temperatures from weather stations. Finally, the methods of Dennis and Kemp (1988) were used to estimate the occurrence of 7 important grasshopper phenological events that are driven by degree days (Fig. 1). Degree day occurrence dates for grasshopper development were then converted to Julian dates so that grasshopper phenological and plant phenological events could be compared. In the case of the estimated date of occurrence of 75% instar 1 (Fig. 1), we used only those dates which were equal to or greater than the date of the first

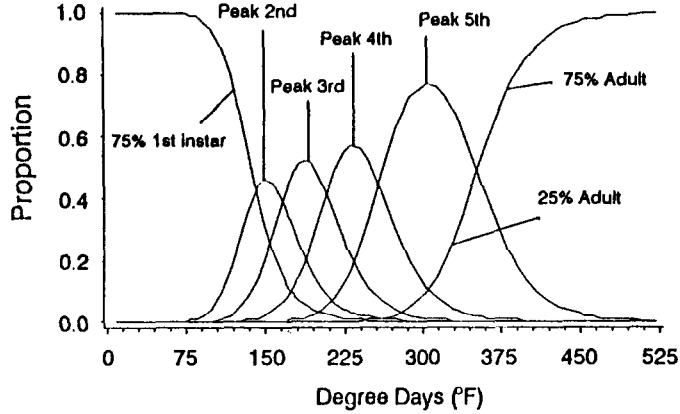


Fig. 1. Example of progression of rangeland grasshopper phenology as estimated by the Dennis-Kemp model (Dennis et al. 1986, Dennis and Kemp 1988).

grasshopper sample date.

Standard ANOVA, stepwise regression, and nonparametric median tests (SAS Institute, Inc. 1988) were used to examine the general relationships between plant phenophases and grasshopper development phases (SAS Institute, Inc. 1988).

Results and Discussion

Plant and Insect Development

The average estimated phenophase dates for purple common lilac and Zabeli honeysuckle are contained in Table 3. Sites were not significant in any of the ANOVAs computed for each phase ($\alpha = 0.05$).

Table 4 presents the average yearly progression of plant and insect development at each site and shows a link between rangeland grasshopper and indicator plant phenological stages. Means over sites and years show the 75% instar 1 stage (spring hatch) for grasshoppers follows the begin bloom phase of purple common lilac by about 10 days. Peak instar 2 was closely linked to the actual date of the end bloom phase of Zabeli honeysuckle, whereas peak instar 3 followed this plant phenological phase by about 10 days. Results also show that peak instar 5 was closely associated with the first red berry phase of Zabeli honeysuckle. An interesting result is that, on average, peak instar 5 and 25% adult stages occur at approximately the same date. This means that the highest proportions of the fifth instars were found at the time when about 25% of

Table 3. Average estimated phenophase dates and standard deviations () of purple common lilac and Zabeli honeysuckle at 9 sites in Montana, 1986–1988.

Location	Average ¹ estimated Julian date for		
	Begin bloom purple common lilac	End bloom Zabeli honeysuckle	First red berry Zabeli honeysuckle
Glasgow	128(7.5)	144(7.6)	172(4.6)
Havre	124(6.0)	143(5.1)	170(3.5)
Miles City	124(6.4)	147(14.2)	174(10.4)
Jordan	127(9.2)	149(18.4)	178(12.0)
Fort Benton	126(8.5)	142(9.0)	170(5.1)
Broadus	131(10.8)	150(7.5)	177(5.6)
Billings	125(9.0)	146(11.1)	173(8.2)
Great Falls	134(10.0)	150(11.1)	179(6.8)
Three Forks (DCP)	132(9.3)	154(8.7)	181(6.8)
All sites and years	128(7.9) (May 8)	147(9.3) (May 27)	174(7.0) (June 23)

¹Estimated phenophase dates are based on a 3-year average, 1986–1988.

the population was in the adult stage. Lastly, the 75% adult stage followed the first red berry of Zabeli honeysuckle by about 14 days.

Over all years and sites, standard deviations ranged between 7 and 11 days. While individual sites showed differing levels of variability, the progression of insect development, on average, was similar to patterns estimated previously (Onsager 1983). Over the 24–26 site-years evaluated, peak instar 2 followed 75% instar 1 by about 8 days, and peak instars 2 and 3 and peak instars 4 and 5 were separated from one another by an average of 12 and 10 days, respectively. Comparisons made between the timing of grasshopper development stages within plant phase showed significant differences in all cases but one ($P \leq 0.05$, $n = 24$ or 26, Median test, SAS Institute, Inc. 1988). There was no significant difference between the timing of peak instar 5 and 25% adult stages in terms of the number of days following the first red berry phase of Zabeli honeysuckle ($P \geq 0.05$, $n = 26$, Median test, SAS Institute, Inc. 1988).

The results of the present study were similar to a smaller study at one site in 1975–1976 (Kemp 1987), where the end bloom phase of Zabeli honeysuckle preceded peak instar 3 rangeland grasshoppers by about 10 days. Table 4 shows that for 26 site-years, the end bloom phase of Zabeli honeysuckle also preceded peak instar 3 by about 10 days.

Table 4. Mean differences and standard deviation () in days between estimated occurrence dates of indicator plants, purple common lilac and Zabeli honeysuckle, and selected estimated occurrence dates of rangeland grasshopper phenological stages¹.

Location	Years	Days following the begin bloom phase of purple common lilac until				Days following the end bloom phase of Zabeli honeysuckle until			Days following the first red berry phase of Zabeli honeysuckle until			
		75% Instar 1	Years	Peak Instar 2	Peak Instar 2	Peak Instar 3	Peak Instar 4	Peak Instar 5	25% Adult	75% Adult		
Glasgow	3	10(4.7)	3	21(7.5)	4(5.7)	13(7.5)	-7(3.5)	4(3.8)	4(4.2)	6(6.81)		
Havre	3	1(3.2)	3	19(2.5)	0(3.8)	17(2.9)	0(2.0)	9(2.6)	10(1.5)	20(4.2)		
Miles City	1	8(—)	3	8(13.6)	-14(9.5)	2(9.5)	-13(5.2)	-3(5.9)	-3(5.7)	8(4.6)		
Jordan	2	14(4.2)	2	26(6.4)	3(15.6)	16(16.3)	-6(7.8)	5(9.9)	8(7.8)	21(7.8)		
Ft. Benton	3	10(9.0)	3	21(12.7)	5(13.7)	15(10.5)	-4(7.6)	7(6.6)	8(6.1)	19(10.1)		
Broadus	3	7(13.3)	3	14(10.8)	-5(3.8)	9(9.5)	-11(6.6)	-2(5.0)	-1(4.0)	10(7.5)		
Billings	3	11(4.6)	3	17(0.6)	-3(2.6)	11(5.5)	-8(5.9)	0(4.2)	-1(4.6)	9(6.4)		
Great Falls	3	12(13.1)	3	23(13.7)	7(15.7)	16(15.1)	-2(12.3)	8(15.0)	8(13.7)	22(14.0)		
Three Forks (DCP)	3	7(2.1)	3	11(2.0)	-11(3.5)	-3(6.7)	-19(7.2)	-10(5.5)	-9(5.5)	1(9.5)		
All sites and years	24	10(7.0)	26	18(9.4)	-2(10.4)	10(10.5)	-8(8.1)	2(8.5)	3(8.1)	14(9.8)		

¹Six selected species used by Kemp and Onsager (1986), *Ageneotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Aulocara elliotti* (Thomas), *Melanoplus infantilis* Scudder, *M. packardi* Scudder, *M. sanguinipes* (F.).

Variation from site to site for the 3 years of the study suggests that additional factors other than heat probably influenced the observed relationship between plant phenology phases and rangeland grasshopper development (see standard deviations, Table 4). For example, the site that was consistently the earliest, grasshoppers relative to plants, was Three Forks. As noted previously, we used a selected assemblage of 6 common economic grasshopper species at each site (Kemp and Onsager 1986, Kemp 1987). While Three Forks had the highest percent of the population in the 6-species assemblage (Table 5), on average more than 73% of those populations consisted of 1 species, *Aulocara ellioti* (Thomas). Studies by

Table 5. Percent of rangeland grasshopper populations made up of 6 selected species, for 9 locations and 3 years, Montana.

Location	Percent of population in 6 species ¹				
	1986	1987	1988	\bar{x}	SD
Glasgow	91	77	85	84.3	7.0
Havre	55	57	74	62.0	10.4
Miles City	88	76	84	82.6	6.1
Jordan	72	86	sparse ² data	79.0	9.8
Fort Benton	95	83	86	88.0	6.2
Broadus	93	87	91	90.3	3.1
Billings	79	82	84	82.7	2.5
Great Falls	89	69	57	71.7	16.2
Three Forks (DCP)	96	95	96	95.3	0.6

¹Six selected species used by Kemp and Onsager (1986), *Ageneotettix deorum* (Scudder), *Amphitornus coloradus* (Thomas), *Aulocara ellioti* (Thomas), *Melanoplus infantilis* Scudder, *M. packardii* Scudder, *M. sanguinipes* (F.).

²Densities too low to make accurate estimates.

Kemp and Onsager (1986) show that *A. ellioti* develop more quickly than most of the other members of the 6-species assemblage and suggest that managers of lands that support higher populations of these species will need to assess and treat earlier.

Implications to Pest Management

Results of this study have implications for the timing of grasshopper management activities in Montana. The advent of purple common lilac bloom should signal to ranchers and pest managers that rangeland grasshopper hatching is underway or will be during the next week or so (also Julian date (JD) 75% instar 1 = 30.36 + .84x₁, where x₁ = the JD of the begin bloom phase of purple common lilac; P = 0.001, r² = 0.51). Peak instar 3, the ideal time to assess rangeland to determine whether there is a problem density (Onsager 1986), occurs on average 10 days after the end bloom phase of Zabeli honeysuckle. In addition to timing of grasshopper development, the results are useful for preparing for appropriate applications of biological or chemical control tactics (Onsager 1986, 1987a, 1987b; Kemp et al. 1988; Berry et al. 1991). Further work on links between vegetation type and grasshopper assemblages (Kemp et al. 1990b) will provide ranchers and land managers with information that will aid in adjusting estimates to local situations.

Frequently, the indicator plants are separated in elevation from the local rangeland grasshopper assemblages. If this difference exceeds 30.5 m, then a lapse rate of about 1 day per 30.5 m difference in elevation should be used. For example, if a rancher observes the begin bloom phase of purple common lilac near his/her home, that plant phase date would be expected about 2 days later at a nearby site 61 m higher in elevation (Tables 1, 3, 4). Additionally, because of heat distribution patterns relative to aspect and slope, managers could expect to see earlier hatching and faster development of grasshoppers on south facing aspects with significant slope.

Additional work will be required to provide for more accurate

phenophase estimates based on slope and aspect, as well as elevation (Jackson 1966). Unfortunately, we were not able to make plant observations on site and had to rely on statistically based estimates of phenophase dates. However, our results show that a practical relationship exists between indicator plant and rangeland grasshopper phenology that has utility for scheduling assessment and management activities. The regression relationship noted above between hatching and the begin bloom phase of purple common lilac can be used to establish an initial reference date each year. Tables 3 and 4 can then be used to estimate when different grasshopper development phases will occur. Because range managers do not commonly have access to equipment for computing degree days, we believe the association between grasshopper development and indicator plant phenology will be useful until more complex tools are available. Further, although indicator plant phenology integrates information relative to springtime heat accumulation in a given year, variation in dates between years for a given site can be larger than the overall standard deviations in Table 3. For example, 75% instar 1 occurred, on average, about 16 days earlier in 1987 compared to 1986. Additionally, the plant phenophase dates also averaged 16 days earlier in 1987. In a specific example for Billings during 1986, if the mean date of begin bloom for purple common lilac from Table 3 were used (125) instead of the "observed" date (134), grasshopper phenology estimates would be early by 9 days. Therefore, we suggest that actual plant observations be made instead of simply using the mean values for plant phase dates contained in Table 3. Depending on their location, resource managers may find that local situations more closely follow one of the individual sites in Table 4 rather than the overall means.

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Light reflectance characteristics and video remote sensing of pricklypear

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Abstract

This paper describes the use of a black-and-white visible-infrared ($0.4\text{--}2.4\ \mu\text{m}$) sensitive video camera, filtered to record radiation in the $1.45\text{--}2.0\ \mu\text{m}$ mid-infrared (MIR) spectral region, for distinguishing the succulent plant species pricklypear (*Opuntia lindheimeri* Engelm.) on rangelands in southern Texas. Ground-based spectroradiometric plant canopy measurements at 5 sampling dates revealed that pricklypear had significantly lower ($p = 0.05$) reflectance than that of associated plant species and soil over the $1.50\text{--}1.75\ \mu\text{m}$ MIR water absorption spectral region. Airborne MIR video imagery of rangeland areas indicated that pricklypear populations could be differentiated from other landscape features. The optimum time for distinguishing the evergreen pricklypear was in January–February because most of the associated woody plant species were deciduous and lost their foliage during this period. Computer-based image analyses of MIR video imagery showed that pricklypear populations could be quantified, indicating that MIR video imagery may be useful for distinguishing and mapping pricklypear populations over large and inaccessible rangeland areas.

Key Words: video remote sensing, spectral characteristics, range management, *Opuntia*

Pricklypear (*Opuntia lindheimeri* Engelm.) is a succulent shrub 1–3 m high found on rangelands of south and west Texas and northeastern Mexico (Correll and Johnston 1970). It is often a troublesome species that forms dense stands up to 10 m across. Pricklypear is especially troublesome on poor condition or sparsely covered grasslands where it spreads rapidly because the cladophylls (pads) or branches and seed that have passed through birds

and animals can readily become established on bare ground (Smith and Rechenthin 1964). It is difficult to control by mechanical means, especially root plowing, because this method breaks up and spreads the cladophylls, which often drastically increase the stand density. Broadcast sprays or granular herbicides offer the most promising control methods for pricklypear (Scifres 1980).

Although pricklypear can create a serious brush problem on rangeland, it is a beneficial plant to wildlife and livestock. Pricklypear provides protection for quail and other birds (Scifres 1980, Lehmann 1984), and the fruit and cladophylls are eaten by several species of birds and animals (Vines 1960, Arnold and Drawe 1979, Everitt et al. 1981a, Lehmann 1984). It is also browsed by cattle (Everitt et al. 1981b) and is often used as an emergency feed in drought times or winter after burning off the spines (Smith and Rechenthin 1964, Scifres 1980). Pricklypear is not inherently nutritious, but Gonzalez (1989) recently reported that N and P fertilization can be used to increase the nutritive value and productivity of pricklypear.

Water in plant leaves is a strong absorber of infrared light particularly over the 1.35 to $2.5\ \mu\text{m}$ middle-infrared (MIR) water absorption region of the electromagnetic spectrum (Gates et al. 1965, Knipling 1970). Visible, near-infrared (NIR), and MIR reflectance measurements revealed that the MIR water absorption region was best for distinguishing between succulent and nonsucculent plant species (Gausman et al. 1977, 1978; Everitt et al. 1986c). This is a spectral region that photographic film (black-and-white and color-infrared) is not sensitive to because its sensitivity terminates at the $0.90\ \mu\text{m}$ wavelength. Everitt et al. (1987) reported that a black-and-white video camera with MIR (1.45 to $2.0\ \mu\text{m}$) sensitivity could be used as a remote sensing tool to distinguish the succulent crop plant species onions (*Allium cepa* L.) and aloe vera (*Aloe barbadensis* Mill.) from nonsucculent crop plant species. The objective of this study was to determine the feasibility of

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Thanks are extended to Rick Villarreal for his expertise with image processing, Joe Gallardo for preparation of figures, and Saida Cardoza and Carol Harville for typing the manuscript.

Manuscript accepted 27 December 1990.

using airborne MIR video imagery to distinguish pricklypear on south Texas rangelands. The ability to remotely distinguish pricklypear over large and inaccessible rangeland areas would be beneficial to range managers and wildlife ecologists. This information would be beneficial to range managers to monitor the spread or contraction of pricklypear over time, delineate areas needing control, and for mapping areas of reserve livestock forage during drought. Wildlife managers would benefit by having the capability to map areas of wildlife habitat.

Materials and Methods

This study was conducted in rangeland areas of south Texas. Study sites were located near Alice, Campbellton, Edinburg, Mercedes, and Weslaco in the Rio Grande Plain resource area (Gould 1975). Ground reflectance measurements, aerial video imagery, and ground truth data were conducted for this study. Ground truth observations were made to verify video imagery, whereas reflectance measurements were made to interpret the imagery. Video imagery and reflectance measurements were obtained of pricklypear infested rangelands at different dates during the growing season to determine the optimum time of year to distinguish pricklypear from associated plant canopies.

Reflectance measurements were made near Weslaco, Texas, using a large truck-based Exotech¹ spectroradiometer (Leamer et al. 1973) in August and November 1989 and January, February, and May 1990. Reflectance measurements were made on pricklypear, huisache [*Acacia farnesiana* (L.) Willd.], honey mesquite (*Prosopis glandulosa* Torr.), mixed herbaceous species, and bare soil. Huisache and honey mesquite are woody plant species that often occur in association with pricklypear, whereas the dominant herbaceous species are usually comprised of mixtures. Major herbaceous species were buffelgrass (*Cenchrus ciliaris* L.), sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], hooded windmill-grass (*Chloris cucullata* Bisch.), common bermudagrass [*Cynodon dactylon* (L.) Pers.], and western ragweed (*Ambrosia psilostachya* DC). Measurements were not made on huisache and honey mesquite in January and February because they are deciduous species that lose their leaves in winter. Reflected radiation was measured on each of 7 randomly selected plant canopies (each species or mixture) or soil surfaces on each date at 0.05 μm increments over the 0.45 to 2.45 μm spectral region with a sensor that had a 15-degree field-of-view placed approximately 3.0 m above each target. The sensor was mounted on a Truco aerial lift ("cherry picker"). Measurements were made under sunny conditions between 1100 and 1500 hr. Overhead conventional color photographs were taken 2–3 m above canopies of the various species and mixtures of species to help interpret canopy reflectance data.

The video equipment consisted of 1 MII 2500 video camera, 2 Cohu 4810 video cameras, and 3 Panasonic AG-7400 Super-VHS portable video cassette recorders (1/2-inch format, 400 horizontal line resolution). The MII camera had a specially designed lead oxide (PbO)—lead sulfide (PbS) camera tube (1.0-inch format) to give visible-infrared light (0.4–2.4 μm) sensitivity. A filter combination of 2 long wavepass filters allowing transmittance of light from the 1.45–2.0 μm were used on the MII camera (Everitt et al. 1986a), giving it sensitivity in the MIR water absorption region. The Cohu cameras had charge coupled device (CCD) image sensors (0.7-inch format) with visible/NIR (0.4–1.1 μm) sensitivity. One of the Cohu cameras was equipped with a NIR (0.815–0.827 μm) narrowband filter plus a 0.5 neutral density filter. The second Cohu camera was equipped with a red (0.644–0.656 μm) narrowband filter. All cameras had Canon zoom lenses which were set at

40-mm focal lengths. Differences in lens optics, sensor types and format between the MIR tube camera and the red and NIR CCD cameras caused the imagery to have slightly different fields-of-view.

Video recordings were obtained near Alice, Campbellton, Edinburg, and Mercedes, Texas. Imagery was acquired near Alice and Campbellton in August and November 1989 and January and February 1990, and near Edinburg and Mercedes in May, June, August, and October 1989. Additional imagery was taken near Edinburg in January 1990. Although the imagery dates did not all coincide with the ground reflectance measurement dates, imagery was generally obtained of the plant species during the same phenological stages and vegetative conditions that the plants were in when reflectance measurements were made. Simultaneous recordings of each area were taken using all 3 video cameras. Imagery was obtained at altitudes ranging from 600–1,200 m. All imagery was obtained with a Cessna 206 airplane with the video cameras mounted vertically in the floor. A characteristic of the MIR sensitive camera was persistence of image (image lag) which caused blurring when the camera was moving. This was attributed to its PbO-PbS tube and was more apparent at lower altitudes (600–900 m). To compensate for this the pilot slowed the plane to approximately 70 knots.

Ground-level video recordings were also obtained of pricklypear with the red, NIR, and MIR filtered video cameras to illustrate its spectral light characteristics in each band.

Ground truth data were collected at the study sites at or near the time imagery was obtained. Data were recorded relative to plant species, plant height, density, cover, soil type, and soil surface conditions. Conventional color ground photographs were also obtained at each site.

Middle-infrared video scenes of pricklypear acquired at an altitude of 1,050 m were converted to digital format (512 \times 512 pixel format; digitized ground pixel size of 0.66 m) with an image processing system that consisted of a PC-AT clone computer having a Matrox MVP/AT board and IMAGE-PRO II processing software. Images were subjected to the "index replacement" function which permitted the training of pixels that represented pricklypear in the scenes. This technique permitted the computer to produce a classified binary image that highlighted pricklypear as white pixels and everything else in the image as black pixels. The IMAGE-PRO II "analysis" functions were used to determine the percentage of pricklypear in each image. Video images shown here were photographed from an image display monitor.

A manual photointerpretive procedure was used on a print of 1 of the digitized MIR scenes of pricklypear to compare differences in classification (Everitt et al. 1988, 1991). A map was made of the print by tracing areas where pricklypear was thought to occur onto a transparent paper overlay of the print. Areas where pricklypear was thought to occur were coded black and the remainder of the map was left white. The tracing was digitized and subjected to the "index replacement" and IMAGE-PRO II "analysis" functions as described above to obtain the percentage of pricklypear in the image.

Plant canopy cover was determined on 3–4 canopies of each plant species or mixture on each date that reflectance measurements were made to help interpret the spectral data. Canopy cover was obtained from the overhead photographs taken of the canopies by subjecting them to a grid technique. This consisted of digitizing a color slide transparency of each canopy and superimposing a grid over it on the image display monitor. Percent cover was calculated from the number of squares occupied by plant tissue. The computer grid was utilized since it was available with the image processing software. Water content was also determined on the different plants at the time of reflectance measurements by collecting 10 leaf/cladophyll samples from each species or mix-

¹Mention of a company name or trademark is for the reader's benefit and does not constitute endorsement of a particular product by the U.S. Dept. of Agriculture over any others that may be commercially available.

tures. Each sample was a composite from 3 plants. Leaves/cladophylls were enclosed in plastic bags, stored on ice to minimize dehydration, and transferred to the laboratory for measurements. Pricklypear cladophylls were cut into strips before measuring water content to help expedite the drying process. Percent water content are reported on an oven dry weight basis (68° C for 72 h).

Reflectance data were calculated from the wavelengths that most closely corresponded to the filters used to acquire the video images. These included the 0.65 μm for the visible red, the 0.80 and 0.85 μm for the NIR, and the 1.50, 1.55, 1.60, 1.65, 1.70, and 1.75 μm for the MIR water absorption region. The mean reflectances were computed for the 0.80 and 0.85 μm and 1.50, 1.55, 1.60, 1.65, 1.70, and 1.75 μm wavelengths to represent the NIR and MIR spectral regions, respectively. Duncan's multiple range test was used to test the statistical significance at the 0.05 probability level among means (Steel and Torrie 1980).

Results and Discussion

Light reflectance values of pricklypear, 2 associated plant species, mixed herbaceous species, and soil within 3 wavelength intervals for 5 sampling dates are given in Table 1. In August and

Table 1. Mean light reflectance measurements of pricklypear, honey mesquite, huisache, mixed herbaceous species, and soil for the visible, near-infrared, and mid-infrared wavelength intervals. Measurements were made on 5 dates for bare soil, mixed herbaceous species and pricklypear. Honey mesquite and huisache are deciduous species and were not available for measurements in January and February 1990. Reflectance measurements were made near Weslaco, Texas.

Date	Plants and soil	Reflectance values ^a		
		0.65	0.80–0.85	1.50–1.75
August 1989	Bare soil (crusted)	15.0 a	24.2 bc	39.3 a
	Honey mesquite	2.3 d	31.5 a	11.5 d
	Huisache	3.3 c	31.5 a	15.5 c
	Mixed herbaceous species	6.4 b	21.7 c	23.7 b
	Pricklypear	5.9 b	25.5 b	8.4 e
November 1989	Bare soil	13.1 a	18.8 d	33.6 a
	Honey mesquite	3.0 c	25.3 ab	11.8 d
	Huisache	4.3 c	23.2 bc	16.1 c
	Mixed herbaceous species	6.9 b	20.1 cd	27.3 b
	Pricklypear	5.5 bc	27.2 a	8.9 e
January 1990	Bare soil	10.9 a	19.8 b	35.9 a
	Mixed herbaceous species	7.0 b	20.9 b	30.1 b
	Pricklypear	6.1 c	23.3 a	7.3 c
February 1990	Bare soil	10.7 a	18.5 c	32.1 a
	Dormant herbaceous species	10.7 a	17.7 c	27.7 b
	Mixed herbaceous species (green)	5.8 b	27.2 a	25.9 b
	Pricklypear	5.9 b	23.0 b	7.5 c
May 1990	Bare soil (crusted)	18.4 a	28.8 ab	43.7 a
	Honey mesquite	2.5 d	30.9 a	12.1 c
	Huisache	3.1 cd	26.4 bc	13.7 c
	Mixed herbaceous species	6.7 b	25.2 cd	24.1 b
	Pricklypear	4.5 c	22.8 d	5.9 d

^aValues within columns at each date of sampling followed by the same letter do not differ significantly at the 0.05% probability level according to Duncan's multiple range test.

November 1989, the visible (0.65 μm) and NIR (0.80–0.85 μm) reflectance values of pricklypear did not differ from that of several associated plant species. The inability to separate pricklypear from associated species at the visible wavelength was attributed to sim-

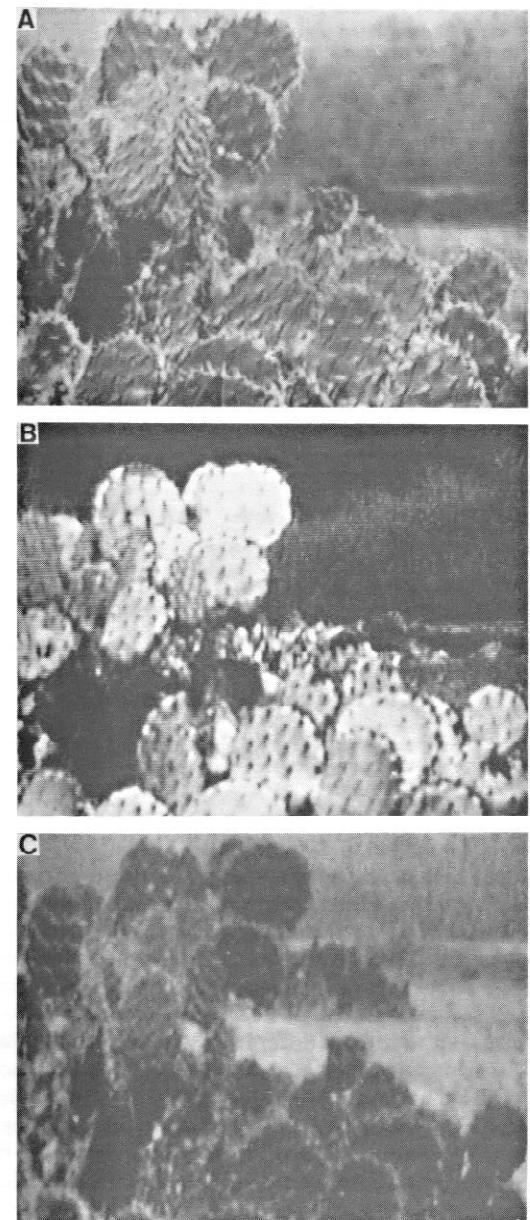


Fig. 1. Red (A), near-infrared (B), and mid-infrared (C) ground video images of pricklypear in a rangeland area near Weslaco, Texas.

ilar foliage colors among the species (Myers et al. 1983). Pricklypear had a gray-green to green color that was comparable to that of mixed herbaceous species on both dates and to that of the associated species in November. At the NIR (0.80–0.85 μm) wavelength pricklypear had a reflectance value similar to bare soil in August, and similar to honey mesquite in November.

In vegetation, NIR reflectance is highly correlated with plant density (Myers and Allen 1968, Wiegand et al. 1974, Everitt et al. 1986b). Phytomass measurements were not made, but plant cover data (Table 2) indicated that pricklypear cover was similar to that of both honey mesquite and huisache in November. This parameter probably contributed to the similarity of reflectance values on that date. Mean reflectance measurements over the 1.50–1.75 μm (Table 1) MIR water absorption spectral region in August and November showed that pricklypear had significantly lower reflectance than all other canopy conditions on both dates. The lower MIR reflectance values of pricklypear were attributed to its higher water content (Table 2) than that of the other plant species which

Table 2. Mean leaf or cladophyll water content and canopy cover of pricklypear and associated plant species on 5 dates.

Date	Plant species or mixture	Water content (%)	Canopy cover (%)
August 1989	Honey mesquite	58.1 ± 1.2 ^a	91 ± 2.5
	Huisache	58.5 ± 1.0	95 ± 2.6
	Mixed herbaceous species	67.1 ± 1.3	63 ± 8.0
	Pricklypear	87.7 ± 1.7	80 ± 3.0
November 1989	Honey mesquite	63.4 ± 1.2	75 ± 5.0
	Huisache	62.9 ± 1.6	78 ± 8.5
	Mixed herbaceous species	60.5 ± 1.5	60 ± 7.0
	Pricklypear	91.9 ± 1.0	73 ± 4.5
January 1990	Mixed herbaceous species	40.4 ± 3.5	51 ± 7.5
	Pricklypear	91.2 ± 0.5	74 ± 8.2
February 1990	Dormant herbaceous species	14.6 ± 5.6	53 ± 10.2
	Mixed herbaceous species (green)	78.4 ± 1.5	83 ± 7.0
	Pricklypear	88.3 ± 0.8	69 ± 8.0
May 1990	Honey mesquite	60.9 ± 1.2	85 ± 6.9
	Huisache	59.1 ± 0.6	79 ± 6.7
	Mixed herbaceous species	69.6 ± 2.9	75 ± 5.2
	Pricklypear	93.2 ± 0.5	67 ± 10.4

^aStandard deviation.

caused it to absorb a larger percentage of the MIR radiation (Gates et al. 1965; Gausman et al. 1977, 1978).

In January 1990, pricklypear had significantly lower visible (0.65 μm) reflectance than mixed herbaceous species and soil, whereas its NIR (0.80–0.85 μm) reflectance was higher than that of mixed herbaceous species and soil (Table 1). Pricklypear had significantly lower MIR (1.50–1.75 μm) reflectance than mixed herbaceous species and soil in January. In February 1990, the visible reflectance of pricklypear did not differ from that of mixed herbaceous species. At the NIR wavelengths, however, pricklypear had a significantly different reflectance value than that of the associated species and soil. The MIR reflectance of pricklypear was lower than that of the associated species and soil in February. For the May 1990 sampling date, pricklypear had a visible reflectance value similar to that of huisache, while its NIR reflectance did not differ from that of mixed herbaceous species. In the MIR range, however, the reflectance value for pricklypear was significantly lower than for all other canopy conditions. Although pricklypear had distinct visible and NIR reflectance on some of the sampling dates (January and February), the spread between its mean reflectance values and that of the associated plant species and soil was not as great as in the MIR spectral region for the January, February, or May study periods. The distinct separation of pricklypear in the MIR spectral region on all dates is attributable to its greater water content on all dates (Table 2). These data indicate that the MIR spectral region is best for distinguishing pricklypear from associated vegetation and soil.

Figure 1-A, B, and C show red, NIR, and MIR ground video images, respectively, of pricklypear in a rangeland area near Weslaco, Texas. In the visible red image (Fig. 1A) pricklypear has a gray tone which is attributed to absorption by chlorophyll in this part of the spectrum (Myers et al. 1983), whereas in the NIR band (Fig. 1B) pricklypear has a whitish-gray response because green vegetation is reflective in this spectral region (Myers and Allen 1968). The dark gray to almost black tone of pricklypear in the MIR video image (Fig. 1C) is attributed to its succulent tissue and

subsequent high water content (Table 2) which absorbed a large percentage of the MIR radiation (Gausman et al. 1978, Everitt et al. 1986a).

Red, NIR, and MIR aerial video images of a rangeland site populated with pricklypear are shown in Figures 2-A, B, and C, respectively. The imagery was obtained in January 1990 near Alice, Texas. The arrows on the images point to a stand of pricklypear plants. Other pricklypear plants are scattered throughout the images. No other shrubs are detectable in the images because they are deciduous in winter. In the red image (Fig. 2-A) pricklypear has a variable gray signature that can generally be detected, but some plants are difficult to distinguish from the lighter gray background signature of mixed herbaceous vegetation. Soil has a whitish gray signature. Pricklypear has a gray to light gray signature in the NIR image (Fig. 2-B) that is difficult to separate from the associated mixed herbaceous species and soil. In the MIR image (Fig. 2-C) pricklypear has a dark gray to black image tone that can generally be separated from the gray and whitish tones of mixed herbaceous species and soil, respectively. The high water content of pricklypear apparently contributed greatly to its pronounced dark signature in the MIR image (Gausman et al. 1977, 1978), but in-canopy shadowing probably also attributed to its dark image response (Richardson et al. 1975).

Ground truth surveys from 7 scattered sites selected from MIR video images of rangeland areas near Alice, Campbellton, Edinburg, and Mercedes, Texas, in January and February 1990 resulted in correct visual identification of pricklypear at all locations. Pricklypear had a similar image response at all locations and could be distinguished best on imagery acquired at 900–1,200 m (recorded horizontal ground pixel size 0.75–0.95 m). Pricklypear could be distinguished in some of the visible red imagery obtained at these locations, but its signature was not as distinct as that in the MIR imagery. An analysis of the NIR imagery from these areas showed that pricklypear usually could not be distinguished in this spectral band.

Figure 2-D shows the computer classification of the MIR (Fig. 2-C) video image. Pricklypear has a white code in the computer classification. A visual comparison of the computer-classified MIR image to the conventional MIR image showed that the computer generally identified most of the pricklypear plants. The computer estimated that 3.9% of the image was pricklypear, whereas the computer estimated that 5.0% of the photointerpreter's overlay map of the area was made up of pricklypear. Ground truth data indicated that the photointerpreter's estimate of pricklypear cover was probably more accurate than the computer estimate in this instance. The computer did not identify some of the small pricklypear plants that were visible to the photointerpreter. However, the disagreement could also be contributed to the training of the photointerpreter since subjective boundary lines are drawn due to the grading of pricklypear and soil or herbaceous plant species from one to another. Nonetheless, these results indicate that pricklypear populations can be quantified on MIR video imagery.

Although pricklypear had significantly lower MIR (1.50–1.75 μm) canopy reflectance (Table 1) than all other canopy conditions on all dates, it could not always be distinguished on aerial MIR imagery. We found that in-canopy shadowing of honey mesquite, huisache, and other associated shrubs often produced a dark gray to black signature that made it difficult to distinguish pricklypear from these species during the growing season. Pricklypear could usually be separated from the larger woody plant species by its typical round shape and smaller stature, but small shrubs and pricklypear often had a similar MIR signature. A qualitative analysis of the red and NIR imagery obtained during the growing season showed that pricklypear usually could not be differentiated in these spectral bands. Thus, our findings indicate that the opti-

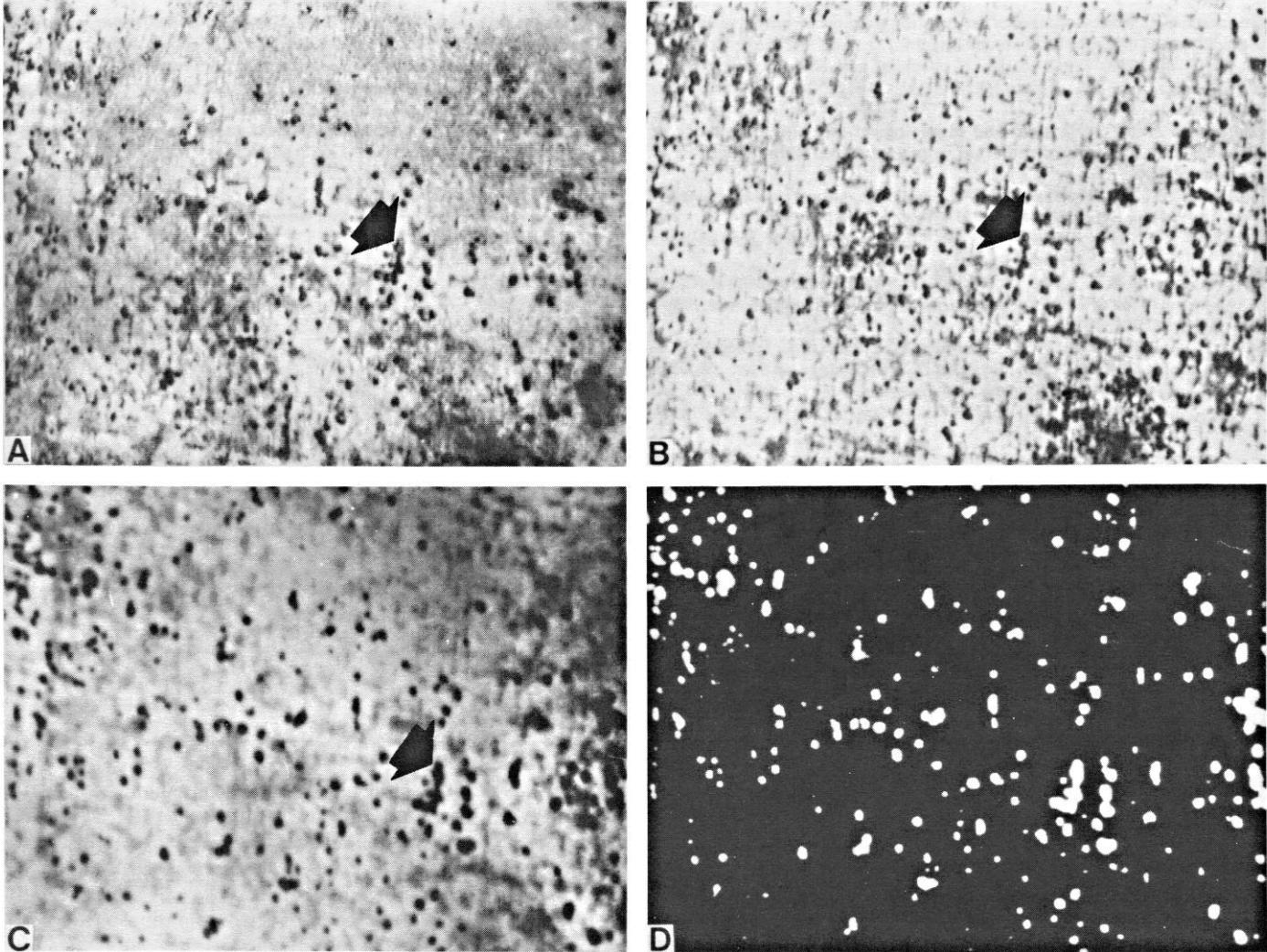


Fig. 2. Red (A), near-infrared (B), and mid-infrared (C) aerial video images of a rangeland area populated with pricklypear and computer classification (D) of the mid-infrared image. The imagery was acquired at an altitude of 1,050 m near Alice, Texas on January 25, 1990.

mum time to do MIR video aerial surveys to distinguish pricklypear would be in the January–February period when the majority of associated woody plant species lose their foliage.

Conclusions

Our results indicate that MIR video imagery may be a potentially useful tool to remotely distinguish pricklypear populations from other cover types on south Texas rangelands. Aerial surveys should be made in January–February when most associated woody plant species lose their foliage. Image analyses showed that pricklypear populations could be differentiated quantitatively. The capability to remotely distinguish and quantify pricklypear on rangelands should be useful to range and wildlife resource managers who are interested in monitoring its distribution and population.

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Sward and steer variables affecting feasibility of electronic intake measurement of grazers

JAMES R. FORWOOD, ANA M.B. da SILVA, AND JOHN A. PATERSON

Abstract

Forage intake is perhaps the most critical parameter in understanding performance of ruminants on pasture. The Thermal Conductivity Cannula (TCC) is an animal-carried device that measures forage intake without disturbing normal grazing patterns by counting the number of boli swallowed over time. To evaluate its accuracy, studies of the effects of animal size, forage availability, quality, and species differences were conducted. In a grazing study, bolus weights of heavy (533 kg) and light (360 kg) esophageally fistulated steers were monitored on 2 different grazing systems [tall fescue (*Festuca arundinacea* Shreb) + red clover (*Trifolium* sp.) season-long vs. tall fescue + red clover in spring and fall and big bluestem (*Andropogon gerardi* Vit; cv. Kaw) in summer]. Boli weight differences between steer weights indicated that TCC intake estimation will require calibration for steer weight or use of uniform steers. Boli weights of heavy steers varied ($P < 0.05$) within (9.0 to 19.4 g) and among (19.4 to 30.2 g) forage species. That did not occur with light steers ($R = 6.25$). Analysis of data on a metabolic weight basis indicated that size of the oral cavity and the 'critical mass' needed to stimulate swallowing may be a factor as well as weight. Sward characteristics and quality parameters were poorly correlated with bolus weight. An indoor study using 3 steer weights (heavy-546 kg, medium-486 kg, and light-220 kg) fed orchardgrass (100%), alfalfa (100%), and orchardgrass \times alfalfa hay (50/50) indicated that heavier steers always produced heavier boli but that the weight differences between steers had to be greater than 86 kg to be significantly different. Light steers produced most consistent boli weights over all feeds.

Key Words: ingestion, deglutition, grazing ruminants, forage-livestock

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Joint contribution of USDA-ARS and the Dept. of Agronomy, University of Missouri, Columbia 65211.

Manuscript accepted 27 April 1991.

Animal performance on pasture is largely a function of animal requirement, concentration, and availability (digestibility) of nutrients multiplied by forage intake. Whereas the digestibility and metabolizability of the diet consumed may vary by a factor of about 2, herbage intake of ruminants may vary by a factor of at least 4, even under relatively unrestricted conditions (Hodgson 1982). This statement underscores the importance of understanding the factors which regulate intake and more importantly, the need for more accurate intake measurement.

Attempts of a more direct nature than the traditional total fecal collection or indicator methods have been made recently to measure herbage intake of free roaming livestock. The Animal Weight Telemetry System (AWTS; Horn and Miller 1979) and multiple electrode impedance plethysmography (Stuth et al. 1981) system are examples of potential animal-carried devices that reduce handling of livestock and allow undisturbed grazing behavior.

The Thermal Conductance Cannula (TCC; Forwood and Hulse 1987) is an animal carried device which estimated intake by counting the number of boli swallowed by cattle. In-house studies with cattle fed various levels of forage show the number of boli swallowed to be highly correlated with intake ($r^2 = .99$) (Forwood and Hulse 1987). The assumption is made that boli are relatively uniform, with differences in boli weight between grazing initiation and cessation being rather self-compensating. However, questions concerning the effect of animal weight, forage availability, quality, and species on bolus weight needed to be addressed before decisions concerning use of various sized animals and comparisons between varying forage species, qualities, and maturities could be made in the use and efficacy of this device. The present study was designed to investigate the effects of animal and forage species differences on bolus weight as related to the feasibility of electronically measuring intake.

Material and Methods

Grazing Study

This study was conducted within a larger grazing study comparing a Season-Long System (SLS) and a Complementary Grazing System (CGS) (Silva 1987). The SLS involved 2 pastures (all pastures equal 0.81 ha) of endophyte free tall fescue (*Festuca arundinacea* Shreb; MO-96) and red clover (*Trifolium* sp.) with 1 pasture utilized in spring, the second during mid-summer, and the spring pasture grazed again during late-summer and fall. The CGS involved 1 tall fescue + red clover pasture (similar in species to that used in the SLS system) utilized during spring and late-summer or fall period and 'Kaw' big bluestem (*Andropogon gerardi* Vit; cv. Kaw) grazed during mid-summer. The study was conducted at the University of Missouri Agronomy Research Center during 1986 and 1987. Six tester steers (322 kg) grazed the pastures alongside the fistulated steers in order to collect weight gain data.

Three heavy (avg. 533 kg; range = 460 to 620 kg) and 3 light (avg. 280 kg; range = 250 to 300 kg) esophageally fistulated steers (*Bos taurus* L.) were used to determine the relationship between cattle bolus weight and body weights. Fistulated steers were lightly fasted (6–8 hours) the evening before bolus collection. Before bolus collection, esophageally fistulated steers were allowed to graze with their cannulas in place to familiarize them with the pasture and to avoid unusual bolus weight resulting from initial morning grazing. Cannulas were then removed and bolus collection began. Ten distinct boli were collected from each animal as it grazed each treatment pasture. All collections were made within sample periods of 6 consecutive days with each steer receiving 1 or more days of rest between sampling each treatment pasture. The order in which each steer began grazing each treatment pasture on each sample period was randomly assigned. Average weights of the 10 boli were used in analyses. Sample periods were the weeks of 30 May, 15 July, and 11 Aug. 1986, and 20 May, 17 June, 9 July, 11 Aug., and 10 Sep. 1987. Boli were considered distinct when all dimensions of the bolus were visible in order to ensure that all ingested material was exiting the fistula. Boli were placed in individual paper bags, dried at 40° C for 48 hours, weighed, and ground to pass a 1-mm screen (Wiley mill). In vitro organic matter digestibility (IVOMD) was determined on each of the collected boli using a modified 2 stage in vitro technique as described by Marten and Barnes (1980) followed by ashing samples at 500° C for 3 hours and weighing. Crude protein was determined from Kjeldahl N × 6.25 (AOAC 1976). Neutral detergent fiber (NDF) and Acid Detergent Fiber (AFD) were determined using the methods of Goering and Van Soest (1970) without sodium sulfite.

Total dry matter (TDM) was determined by clipping twelve 0.50 m² quadrants per pasture to ground level on or within a few days of the above sample dates. Leaf dry matter (LDM) was determined by hand-separating leaf blades (at the collar) from stems and weighing each component from the above samples. Mean bulk density (BD) (kg KM ha⁻¹ cm⁻¹) was calculated by dividing TDM by the mean sward height (mm) on each sample date. Forty measurements with a meter rule along equally spaced transects throughout the pasture were taken on each sample date and averaged to estimate sward height.

A split plot analysis of variance was used to test differences in boli weights as influenced by steer weights, grazing systems, and periods. Data were analyzed separately each year because of differences in collection dates between 1986 and 1987. The linear statistical model contained the effects of steer weight, steers within steer weights, grazing systems, periods, and all possible interactions of steer weight, grazing systems, and periods. The main effect of steer weight was tested using steer within weight as the denominator of F. All other effects in the model used the Residual Mean Square as the denominator of F. Since most of the comparisons of interest

compare only 2 means, differences were determined using the protected Least Significant Difference (LSD) procedure ($P < 0.05$) (Cochran and Cox 1967). Correlation coefficients were used to test the relationship between boli weights and sward and forage quality parameters.

Indoor Study

Nine esophageally fistulated steers, (*Bos taurus* L.) 3 each of heavy, medium, and light weights (averaging 546, 486, and 220 kg, respectively) were confined to individual pens 2 weeks prior to study initiation at the Animal Science Research Center, University of Missouri, Columbia. Steers were maintained under thermal neutral conditions at all times. They were placed on treatment orchardgrass (*Dactylis glomerata* L.) and alfalfa (*Medicago sativa* sp.) hay diets 2 weeks before data collection. Hay offered to each steer was calculated on the basis of NRC 1984 requirements for beef cattle. A concentrate (1% of body weight) was available to the steers to balance total requirements (81% TDN, 13% protein, 89% CA, and .40% P). Treatment hays tested were orchardgrass (100% of diet), alfalfa (100% of diet), and a 50/50 mixture of the orchardgrass and alfalfa hays on a dry weight basis. Orchardgrass had been harvested at late vegetative stage while the alfalfa was in full bloom at harvest.

Steers were lightly fasted (6 hours) the evening before data collection and were allowed to begin consuming forage with cannulas in place. After a few minutes cannulas were removed and 10 distinct boli were collected from each steer. Average boli weight was calculated from these 10 boli. Boli were allowed to drop on the floor in order to collect them separately. Each bolus was placed in an individual paper bag, oven dried at 40° C and weighed.

Experimental design was three (3×3) Latin squares with rows defined as periods and columns as animals. During each of 3 periods, the steers were fed 1 of the 3 diets. The linear statistical model contained the effects of steer weight, steers within steer weight, period within weight, diets, and the interaction of diets by steer weights. The main effect of weight was tested using steers within weight as the denominator of F. All other effects used the Residual Mean Square as the denominator of F. Each Latin square was defined for a steer weight, while feeds were consistent for all treatment means separated using LSD ($P < 0.05$). Regression analysis was used to determine the relationship between bolus weight and animal weight (Steel and Torrie 1960).

Results and Discussion

Grazing Study

Average bolus weights from heavy and light steers were 14.1 and 5.69 g, respectively, on the SLS system and 21.5 and 8.48 g, respectively on the CGS in 1986 (Table 1); however the 3-way interaction of steer weight × grazing system × period was significant ($P = 0.03$).

Light steers boli weights on the SLS gradually increased ($P < 0.05$) as the 1986 season progressed but no change occurred on the CGS. Heavy steer boli on the SLS were heavier on 15 July ($P < 0.05$) and 11 Aug. ($P < 0.05$) compared to 30 May. Boli from heavy CGS steers 15 July were over twice the weight of boli on 11 Aug. and were significantly ($P < 0.05$) heavier than heavy steer boli on the SLS. No explanation is available from these results, except for sward maturity or species differences due to periods or systems.

For 1987, although the 3-way interaction was not significant, steer weight × grazing system and steer weight × period interactions did significantly ($P = 0.02$ and 0.01, respectively) affect boli weights.

In 1987 average boli weights were 11.8 g and 5.7 g for heavy and light steers, respectively, on the SLS system and 17.5 g and 7.0 g for steers on the CGS system (Table 1).

Table 1. Average bolus dry weights from small and large steers while grazing Season-Long (SLS) and Complementary Grazing (CGS) Systems during the 1986 and 1987 grazing seasons.

Date	Bolus dry weight			
	SLS		CGS	
	Light Steers (300 kg)	Heavy Steers (553 kg)	Light Steers (360 kg)	Heavy Steers (553 kg)
1986	(g)	(g)	(g)	(g)
30 May	2.40	9.05	↑	↑
15 July	5.03	19.39	8.17††	30.2††
11 August	9.64	13.85	8.79††	12.9††

LSD 0.05 = 3.5 for comparisons of means between grazing treatments within steer weights * periods or between periods within steer weights X grazing treatments.
LSD 0.05 = 6.2 for comparisons of means between steer weights within grazing treatments X periods.

Date

1987	(g)	(g)	(g)	(g)
20 May	4.23	9.64	5.05	10.99
17 June	4.89	14.31	5.58††	24.10††
9 July	7.61	10.96	9.33††	14.76††
11 August	5.99	9.60	8.00††	13.96††
10 September	6.10	14.50	7.04	23.74

LSD 0.05 = 5.3 for comparisons of means between grazing treatments within steer weights X periods or between periods within steer weights X grazing treatments.
LSD 0.05 = 8.4 for comparisons of means between steer weights within grazing treatments X periods.

† Missing data

†† Steers were on the big bluestem portion of the Complementary System.

In 1987, heavy steers produced heavier boli than light steers on 17 June and 10 September (Table 1). Means within steer weights over the dates were 4.6, 5.3, 8.5, 7.0, and 6.5 g for light steer boli and 9.8, 19.2, 12.6, 11.8, and 19.2 g for heavy steer boli. While boli weights of light steers did not vary significantly over periods, heavy steers produced heavier boli on 17 June and 10 Sep. than on the other 3 dates. Both of those periods represent a change of pasture and accompanying increases in total available dry matter and leaf dry matter.

Table 1 shows that when steers are grazing pastures of similar species or different species, boli weights of light steers are more similar in weight than those of heavy steers.

Bolus weight for both steer weights was poorly correlated with total herbage dry matter (TDM), leaf dry matter (LDM), sward bulk density (BD), and grazing time (GT) when analyzed in separate systems (Table 2). This poor overall relationship is similar to other findings (Stuth and Angell 1982) which indicated bolus weight is not greatly affected by daily herbage allowance. When sward data from both systems were combined only BD was positively correlated with bolus weight ($r = .66; P < 0.02$) for light steers (data not shown).

Forage quality characteristics were more highly correlated with light steer bolus weights than were sward characteristics (Table 2). However, sward characteristics were highly correlated with light steer boli weights in the CGS. No explanation is available for these results. Boli weight from heavy steers was negatively correlated with ADF in the SLS and positively correlated in CGS systems. John and Reid (1986) speculated that intake may be most limited by physical characteristics of the feed which affect the ease with which it is compressed to form a bolus. This statement was based on their data which showed lighter boli when hay was fed ($\bar{x} = 3.5$ g) than when fresh herbage was fed ($\bar{x} = 12.4$ g). We speculate that, where a negative correlation existed between ADF and boli weight, the herbage may have been difficult to compress with mastication, resulting in lighter boli. When data from both systems were combined and analyzed by animal weight, a positive relationship was

Table 2. Correlation coefficients (r) of light and heavy steer boli weights with total herbage dry matter (TDM), leaf dry matter (LDM), herbage bulk density (BD), grazing time (GT), in vitro organic matter digestibility (IVOMD), neutral and acid detergent fiber (NDF, ADF respectively) and crude protein (CP) averages over 2 years.

Sward physical and quality characteristics	Season-long Tall Fescue	
	Light steers	Heavy steers
TDM	-.25	-.09
LDM	-.10	.61
BD	.43	-.28
GT	.32	-.33
IVOMD	-.60	.41
NDF	.84	.04
ADF	.06	-.63
CP	-.29	-.38

	Complementary grazing system	
TDM	.88	.13
LDM	.89	.15
BD	.81	.13
GT	.77	-.13
IVOMD	-.60	.34
NDF	.67	.16
ADF	.52	.98
CP	.38	-.67

found between bolus weight and NDF. No explanation is available for that phenomena or the inverse relationship between boli weight and IVOMD.

In general, no clear trend is evident between sward and nutritive characteristics and bolus weight. Although there is little previous data relating bolus weight to forage quality and sward characteristics, correlations of grazing time, biting rate, and ingestion rate with similar parameters result in few significant correlations (Olsen et al. 1989). It appears to these authors that cattle may vary bite size, bite rate, and grazing time in attempting to maintain constant intake but those parameters are apparently not reflected in bolus weight.

Boli were heavier in our study for both animal weights tested than the values reported by Stuth and Angell (1982). Their results showed that bolus weight is reasonably uniform throughout a nonrestrictive range of daily herbage allowance, that season has a negligible effect on bolus dry matter weight, and that cow weight did not influence bolus weight. Data from the 2 studies are similar concerning the influence of herbage parameters on bolus weight. Stuth and Angell (1982) mentioned that the cows used in their study represented only moderate to large frame animals (426 and 466 kg; only a 40 kg difference in weight) while the steers used in our study differed by 173 kg in 1986 and 255 kg in 1987.

Although steer weights appear to dictate boli weights, analysis of boli weight data on an animal metabolic weight basis showed ($P < 0.002$) differences for 1986 (7.2 and 17.6 g overall averages for light and heavy steers respectively) and a similar ($P > 0.13$) trend in 1987 (6.5 g and 14.2 g overall averages for light and heavy steers, respectively). Heavy steer boli were also heavier than light steer boli when analyzed as a ratio of boli weight to steer weight (data not shown). We speculate that steer head size (and associated size of the buccal cavity) and the amount of herbage it can accommodate before a 'critical density' or weight stimulates swallowing, may play a part in determining bolus weights. Light steers would obviously reach that point with less dry matter than would heavy steers. Theoretically that would make it possible for a large frame animal in poor flesh to produce a bolus similar to a heavy animal of the same frame.

Equations for adjusting bolus weights for varying steer weights

Table 3. Linear regression equations of the relationship between bolus weight and steer body weights while grazing tall fescue and big bluestem pastures.

	Season-long system	Complementary system
		1986
30 May	$y = 12.53 + .0189 \text{ BW}^{\dagger\ddagger}$ (.06, .86) [†]	(missing data)
15 July	$y = -15.39 + 0.275 \text{ BW}$ (.01, .84)	$y = -24.79 + .0438 \text{ BW}^{\dagger}$ (.006, .87)
11 August	$y = 2.137 + .0096 \text{ BW}$ (.08, .56)	$y = .1488 + 0.011 \text{ BW}^{\dagger}$ (.009, .85)
		1987
20 May	$y = -3.62 + 0.11 \text{ BW}$ (.0002, .53)	$y = -3.09 + 0.114 \text{ BW}$ (.0001, .42)
17 June	$y = -9.69 + 0.02 \text{ BW}$ (.0001, .35)	$y = -22.3 + 0.038 \text{ BW}^{\dagger}$ (.0001, .48)
9 July	$y = .45 + .009 \text{ BW}$ (.0005, .18)	$y = 1.2 + .011 \text{ BW}^{\dagger}$ (.0001, .40)
11 August	$y = 1.27 + .007 \text{ BW}$ (.0001, .30)	$y = 2.64 + .009 \text{ BW}^{\dagger}$ (.0007, .19)
30 September	$y = -4.8 + .015 \text{ BW}$ (.001, .43)	$y = -13.7 + .03 \text{ BW}$ (.001, .59)

[†]Probability of the slope of the line equaling zero and the multiple correlation coefficient (r^2) which equals the percent variation in bolus weight accounted for by a linear function of animal body weight.

[‡]Steers were grazing warm-season grass pasture.

^{††}BW = Steer live body weight (kg)

y = dry material per bolus (2)

for both grazing systems are presented in Table 3. Percentage variation in bolus weight accounted for by a linear function in body weights was greater during 1986 ($x = 76\%$) as compared to 1987 ($x = 38\%$). No explanation is known for this phenomenon.

Indoor Study

Mean boli weights across all hay types for heavy, medium, and light steers were 19.8, 15.1, and 9.7 g, respectively. Heavier animals produced heavier boli than light animals. ($P < 0.05$) Although there were always bolus weight differences between heavy and light steers, bolus weights were not always different between heavy and medium or medium and light steers. There was more similarity in boli weights between heavy and medium than there was between medium and light steers probably due to the fact that there was only 86 kg difference in steer weights between heavy and medium steers compared to 206 kg difference between medium and light steers.

Disregarding steer weights, boli were lightest when alfalfa was fed ($\bar{x} = 12.3$ g) compared to the alfalfa \times orchardgrass mixture ($\bar{x} = 16.0$) or orchardgrass alone ($\bar{x} = 16.3$). This may have been at least partially due to the use of a mature alfalfa containing considerable stem material which was difficult to compress with mastication.

Table 4. Effect of feed type [orchardgrass (OG); alfalfa (ALF.) and the combination of OG \times ALF.] and steer weights on bolus weight (g).

Steer size	Steer weight	Forage	Bolus weight
Heavy	582 (kg)	Alfalfa	15.07 (g)
		OG \times ALF.	24.64
		Orchardgrass	19.66
Medium	496	Alfalfa	12.51
		OG \times ALF.	14.94
		Orchardgrass	17.96
Light	290	Alfalfa	9.38
		OG \times ALF.	8.45
		Orchardgrass	11.22

LSD (0.05) = 3.60

Table 5. Linear regression equations of the relationship between bolus weight and steer body weights when steers were fed orchardgrass, orchardgrass and alfalfa (orch \times alf.)* and alfalfa hays.

Hay	Equation	r^2
Orchardgrass	$y = 5.423 + 0.016 \text{ BW}^{\dagger\ddagger}$.61**
Orch. \times Alf [†]	$y = 1.352 + 0.0402 \text{ BW}$.76*
Alfalfa	$y = 3.478 + 0.0296 \text{ BW}$.58

* Orchardgrass \times alfalfa hay in 50:50 mixture

^{††}BW = steer live body weight

**Significant at 0.05 and 0.01 levels, respectively.

The association between steer weights and boli weights was greater when orchardgrass \times alfalfa hay was fed than with orchardgrass alone or alfalfa alone (Table 5). The interaction of steer weight and feed was significant at ($P < 0.06$). The cause of the interaction appeared to be the very heavy boli produced by heavy steers on the orchardgrass \times alfalfa mixture. Otherwise, the trend was for boli to increase in weight when orchardgrass was added to the diet.

Extrapolating this data to the grazing situation, if one had no alternative but to use steers of various weights when counting boli to determine intake, results may be more accurate on pure alfalfa stands. If one were attempting to estimate intake via boli counting when steers were grazing grass, legume, or grass \times legume combination pastures the data, similar to the outdoor study, we suggest using light steers. This suggestion appears logical because heavy and medium weight steers produced different boli weights on different feeds while light steer boli weights were similar across feeds. This study indicates that at least an 86 kg difference must exist between steer weights for bolus weight to be affected.

Conclusions

If intake were to be estimated by an animal-carried bolus-counting device such as the TCC, our data indicated that experimenters would be required to keep experimental animals within 86 kg of one another. Frame uniformity must also be considered to avoid the potential of thin but large framed animals which may swallow a much larger bolus (and therefore have greater intake) than a heavier but smaller framed animal. Light steers (300 kg range) would be preferable due to the boli weight uniformity between periods and between systems when using light steers. Although sward and forage nutritive quality characteristics did not appear to be correlated with bolus weight, there remains a question concerning bolus weight uniformity over time and between forage species. Either additional studies must be conducted to answer these questions or one or more esophageally fistulated animals similar in size to those carrying the device should be used to periodically measure boli weights and adjust intake estimates accordingly. In any case, more data must be collected before the TCC device can be considered a reliable means of measuring forage intake of free-roaming grazers.

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Nutrient intake of cattle on rotational and continuous grazing treatments

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Abstract

Many benefits have been obtained from rotational grazing, including management flexibility and livestock distribution, but long-term positive effects on plant and animal production have been inconsistent. The purpose of this case study was to investigate nutrient intake of animals in 2 production scale grazing treatments. The study site was the Texas Experimental Ranch located in Throckmorton County, in the eastern portion of the Rolling Plains of Texas. Treatments were a 465-ha, 16-paddock, 1-herd, cell designed rotational grazing system (RG) stocked at a heavy rate ($3.7 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$) and a 248-ha continuously grazed (CG) treatment stocked at a moderate rate ($6.2 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$). Size of RG paddocks was varied to create different livestock densities to simulate rotational grazing at a 14 and 42 paddock level. Comparisons were made to determine the effect of type of grazing system (RG vs. CG) and the effect of livestock density within the RG system on nutrient intake. Nutrient intake of esophageally fistulated steers was determined by daily dosing them with ytterbium nitrate-labeled forage and collection of fecal samples plus collection of fistula extrusa samples for crude protein and in vitro organic matter digestibility determinations. The only difference caused by different livestock densities was a higher ($P < 0.001$) intake of forage crude protein in the simulated 42 paddock system. Nutrient intake of steers in the CG treatment was greater ($P < 0.001$) than those in the RG treatment. Differences between treatment were attributed primarily to differences in stocking rate rather than grazing system.

Key Words: grazing system, livestock density, fecal output, ytterbium

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Appreciation is extended to the Swen R. Swenson Cattle Co. for providing the land, livestock, and facilities for this study and the Texas Experiment Ranch Committee for providing financial assistance.

Report is published with the approval of the Director, Texas Agr. Exp. Sta. as TA-25064.

Manuscript accepted 11 April 1991.

Nutrient intake is regulated by an animal's nutrient requirements, the quantity and quality of feedstuff available, and the animal's inherent ability to harvest nutrients within an energy, time, and bulk constrained environment (Westoby 1974, Ellis et al. 1976, Allison 1985). A major impetus for employing various grazing management strategies on rangelands is to manipulate factors affecting nutrient intake positively to enhance individual animal production and/or production per unit area. A major objective of multi-paddock, single herd rotational grazing strategies (RG) is to increase livestock production per unit area by increasing efficiency of harvest while maintaining nutrient intake and individual animal performance.

The objective of this study was to compare the nutrient intake of cattle on a heavily stocked RG treatment that contained 2 stocking densities, with a moderately stocked continuously grazed treatment (CG). The specific null hypothesis was that nutrient intake would be equal for the 2 treatments regardless of stock density (number of paddocks) in the RG treatment. This study was one of a series of studies designed to quantify the effects of the RG treatment on quantity and quality of forage produced (Heitschmidt et al. 1987a, 1987b, 1987c), diet quality (Walker et al. 1989b), cow/calf production and economic returns (Heitschmidt et al. 1990), watershed condition (Pluhar et al. 1987), number of cattle trails (Walker and Heitschmidt 1986), and several livestock behavioral attributes (Walker and Heitschmidt 1989, Walker et al. 1989a).

Methods

Study Site

The study site was the Texas Experimental Ranch located in Throckmorton County, in the eastern portion of the Rolling Plains of Texas ($99^{\circ} 14' \text{W}$, $33^{\circ} 20' \text{N}$). Climate is continental and semiarid. Average annual precipitation is 680 mm bimodally distributed with peaks in May and September. Average maximum daily temperatures range from 11.4°C in January to 35.8°C in July. Average minimum daily temperatures range from -2.4°C in January to 22.0°C in July.

Soils on the study site are generally deep, well drained, clays and

Table 1. Duration and sequence of nutritive intake trials. The length of the rest period was a function of the estimated growth rate of forage. During dormancy rest periods were about 60 days and during rapid growth rest periods were about 30 days. Graze periods were a function of the rest period, number and size of paddocks in the grazing system.

Length of Graze	Trial dates							
	1982		1983		1984			
	Oct.	Jan.	June	Sep.	Jan.	Mar.	May	Aug.
days								
RG-14	3	4	2	3	4	3	2	3
RG-42	1	1.3	0.6	1	2	1	0.6	1
Length of rest	45	60	30	45	65	45	30	45
Length of trial	9	12	6	9	15	9	6	9

clay loams, with the clay loams predominating. Herbaceous vegetation is a mixture of short- and midgrasses. Dominant shortgrasses are buffalograss [*Buchloe dactyloides* (Nutt.) Engeim.] and common curlymesquite [*Hilaria belangeri* (Steud.) Nash], both warm-season perennials. Dominant midgrasses are sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], a warm-season perennial, and Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.), a cool-season perennial. The dominant annual grass is Japanese brome (*Bromus japonicus* Thunb.). The dominant woody species is honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*). For a detailed description of the climate, soils, range sites, and vegetation at the study site, see Heitschmidt et al. (1985).

Treatments

Treatments consisted of a 465-ha, cell designed RG treatment, established in March 1981, and a single 248-ha pasture CG treatment, established in 1960. Both treatments were stocked with mature Hereford \times Angus crossbred cows and all treatment pastures had a range condition classification of good throughout the study. Rate of stocking in the RG treatment was $3.7 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$ until June 1984 when the stocking rate was reduced to $5.2 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$ because of drought. Stocking rate for the CG treatment was a constant $6.2 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$.

The stocking rate used in the RG treatment was chosen for 2 reasons: (1) previous studies (Heitschmidt et al. 1983) showed that stocking at $3.7 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$ exceeded the carrying capacity of this range under continuous grazing, and (2) one of major reasons for implementing a short duration grazing system was to increase carrying capacity (Savory and Parsons 1980). Continuous grazing at $6.2 \text{ ha} \cdot \text{cow}^{-1} \cdot \text{yr}^{-1}$ was chosen as the control treatment to compare the RG treatment to because it is the recommended stocking rate (Kothmann et al. 1970, Heitschmidt et al. 1982) for continuous grazing at this location and continuous grazing is the most common grazing system in this area.

The RG treatment initially consisted of 14 paddocks that averaged 33 ha in size. In March 1982 one 30-ha paddock was subdivided into three 10-ha paddocks. Data for this study were collected in these three 10-ha paddocks and 2 adjacent 30-ha paddocks. To maintain equal rates of stocking, the length of each grazing period was adjusted by an amount proportional to pasture size. Length of graze in the flexible rotation schedule ranged from 2 to 5 days in the 30-ha paddocks and 18 hours to 2 days in the 10-ha paddocks. Length of rest between grazing periods ranged from approximately 30 to 65 days. The 30-ha paddocks are referred to hereafter as the RG-14 treatment and the 10-ha paddocks are referred to hereafter as the RG-42 treatment because livestock density in the RG-14 and RG-42 paddocks approximate that in a 14- and 42-paddock RG system, respectively. For a more detailed description of the treatments, see Heitschmidt et al. (1987a, 1987c, 1990).

Sampling Procedures

Eight nutritive intake trials were conducted from October 1982 to August 1984 (Table 1). Each trial was conducted as the cattle entered the RG treatment paddocks in their normal rotation cycle. Ten esophageal-fistulated steers were used for both fecal output and diet quality sampling during the first 4 trials. Four intact steers were used to obtain additional estimates of fecal production, for the last 4 trials. They were equally allocated between the 2 treatments. Steers were assigned randomly to treatments for trial 1 and alternated between treatments for each successive trial. Number of steers allocated to treatments varied across trials because of health disorders. Five fistulated steers were always allocated to the RG treatment and the remaining 3 or 4 were used in the CG treatment. This method of distributing animals among treatments was used because conditions in the CG treatment were assumed to remain constant during a trial and the greater number of sample dates was assumed to offset the fewer numbers of animals. The minimal number of animals for any trial was 3 in the CG and 4 in the RG treatments. Steers were pastured with the main cow herds from 1 week before a trial until the end of each trial.

In the RG treatments, diet samples were collected in all paddocks at the beginning and end of each grazing period. An additional mid-grazing period sample was collected in the RG-14 paddocks. In the CG treatment diet collections were taken every other day throughout the trial. Diet collections were made without fasting while the main cow herd was in a major feeding period. Steers, were gathered, fitted with screen-bottomed bags, and returned to graze in the same area as the main cow herd. Extrusa samples were frozen at -15°C and later freeze-dried and ground. They were composited by pasture and date before being analyzed for in vitro digestible organic matter (IVDOM) and crude protein. Percent IVDOM was estimated by a 2-stage procedure for incubating the sample in strained rumen fluid for 48 hours, followed by neutral detergent extraction (Van Soest et al. 1987). Estimates of IVDOM were corrected using the ratio of in vitro/in vivo digestibility of standard forages of known digestibility determined in a feeding trial. The standard forage was pre-bloom oat hay that had in vitro and in vivo digestible organic matter of 58 and 65%, respectively. Percent nitrogen, on an organic matter basis, was determined by the micro-Kjeldahl method (AOAC 1970) and converted to crude protein using a factor of 6.25. A complete description of the diet quality study can be found in Walker et al. (1989b).

Fecal output was estimated using ytterbium nitrate, an indigestible particulate flow marker, in a daily dosing technique (Ellis et al. 1982). Rice hulls were used as a carrier for the ytterbium (Yb), which was administered at the rate of 1.5 g of ytterbium nitrate per 100 kg of body weight. Samples of the marked rice hulls were used to determine actual Yb concentration per dose for each trial. Pretrial dosing was done for 4 days. The steers were gathered each morning, before the main herd's major feeding period, dosed, and

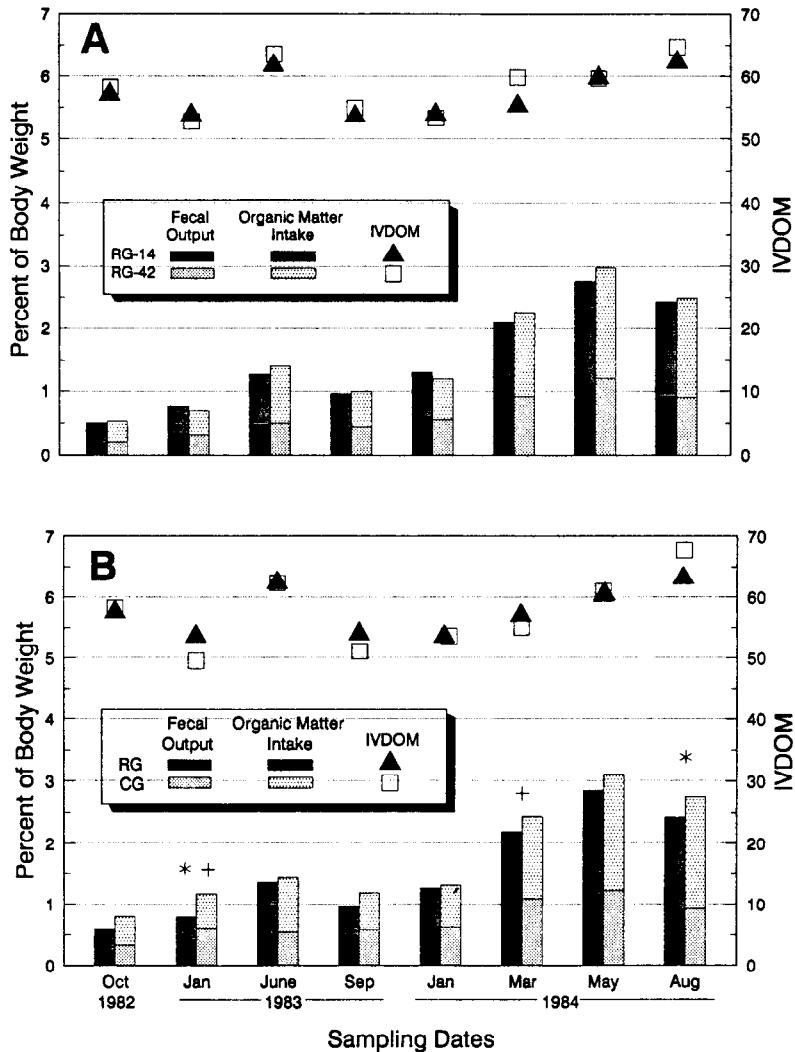


Fig. 1. The affect of livestock density in a rotational grazing treatment (A) or type of grazing treatment (B) on fecal organic matter output (% of body weight), organic matter intake (% of body weight) and diet in vitro digestible organic matter (IVDOM) on 8 sample dates. Dates with asterisks (*) or plus (+) above them indicate that treatment means are different ($P < 0.05$) for OMI and FOMOUT, respectively.

fecal samples collected. Dose and collection times were selected to minimize diurnal variation (Prigge et al. 1981). Fecal samples were dried at 60° C for 48 hours and ground in a Wiley mill to pass a 2-mm screen. Fecal dry matter, organic matter (AOAC 1970), and ytterbium concentrations were then determined. Ytterbium-labeled rice hull and fecal samples were prepared for analysis by solubilizing a 1-g ash sample in 1 normal hydrochloric/nitric acid (Ellis et al. 1982). After filtration and dilution, Yb was determined by atomic absorption spectroscopy using a nitrous oxide/acetylene flame. Ytterbium standards (0 to 5 ppm) were made from pretrial fecal collections that contained no Yb.

Calculations and Statistical Analyses

Daily fecal organic matter output (FOMOUT) was calculated by dividing the actual dose of Yb ($\mu\text{g}/\text{day}$) by Yb concentration in the fecal organic matter ($\mu\text{g}/\text{g}$). Organic matter intake (OMI) was calculated by dividing FOMOUT by the indigestible (100-IVDOM) fraction of the diet. Fecal organic matter output and OMI were expressed as a percent of body weight.

Forage crude protein intake (FCPI) was derived by multiplying the average percent CP of diets (Walker et al. 1989b), times the kg of OMI. Forage metabolizable energy (FMEI),

expressed as $\text{Mcal} \cdot \text{hd}^{-1} \cdot \text{day}^{-1}$, was calculated by multiplying ME concentration (Mcal/kg) in the extrusa by kg OMI. Extrusa DE concentration was calculated using the formula of Rittenhouse et al. (1971) to estimate digestible energy (DE) from IVDOM (i.e., $\text{Mcal DE/kg} = \text{IVDOM} \cdot 0.05 - 0.36$). Digestible energy was converted to ME assuming an 80% conversion efficiency (k_m) of DE to ME. Requirements for FCPI and FMEI were calculated for each trial based on NRC (1984) recommendations for medium frame steers of similar weight and average daily gain as the animals used in this study. Within a trial, daily values of the dependent variables FOMOUT, OMI, FCPI, and FMEI were averaged for each steer. For steers in the RG treatment daily values were averaged separately for the days when the animals were in the RG-14 and RG-42 paddocks to test the effect of livestock density. Data for each steer were averaged across all days and paddocks in the RG treatment to test for the effect of RG compared to CG. These data were analyzed for the effect of grazing treatment, trial and their interaction with steer weight as a covariate. Mean separations were based on single degree of freedom contrast. Individual animals were used as experimental units but were not independent and any inferences made from this grazing treatment case study to a larger population are based on the authors' experience and supporting literature.

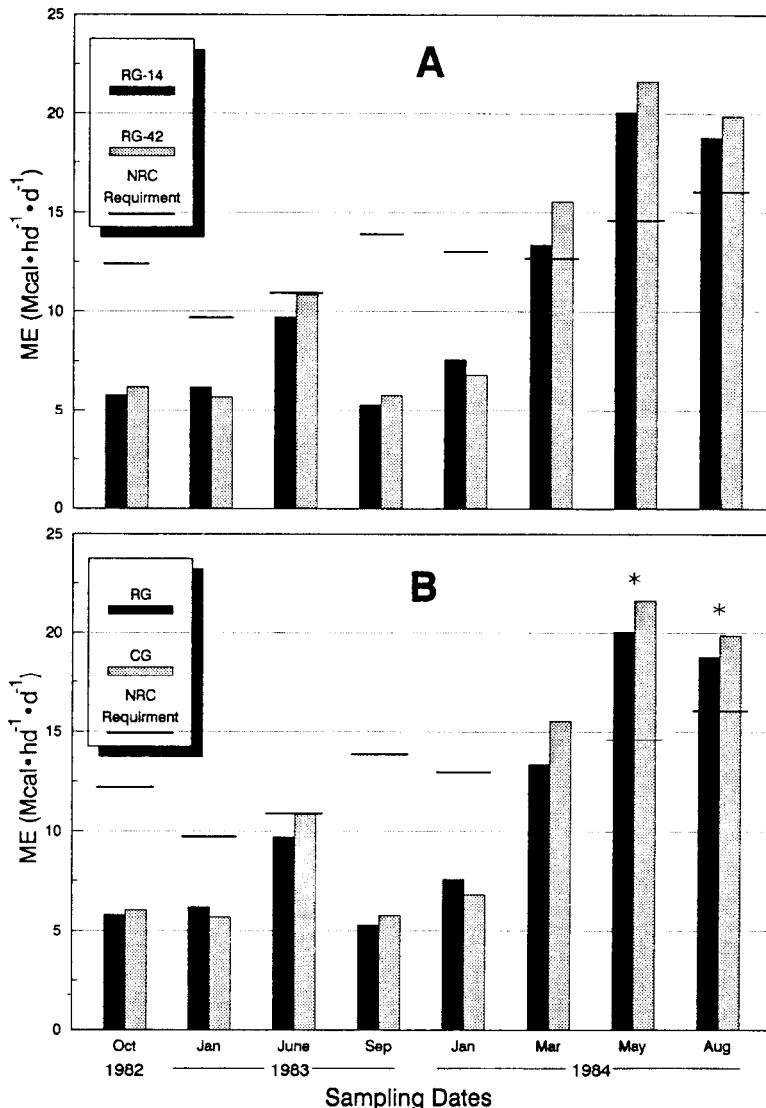


Fig. 2. The effect of livestock density in a rotational grazing treatment (A) or type of grazing treatment (B) on forage metabolizable energy intake on 8 sample dates. Requirements were calculated for each trial using the weight and average daily gain of the steers used to collect nutrient intake data and NRC (1984) recommendations for medium frame steers.

Results

Trial

All response (FOMOUT, OMI, FCPI, and FMEI) variables differed ($P<0.01$) between trials because of the seasonal effects on forage quantity and quality. In general OMI increased as IVDOM increased. There was also an increase in all response variables during the last 3 trials; however, the cause of this increase was not apparent.

RG-14 vs. RG-42

FOMOUT, OMI, and FMEI were not affected ($P<0.98$, 0.36, and 0.09, respectively) by the main effect of stock density within the RG treatment (i.e., RG-14 vs. RG-42; Figs. 1A and 2A). FCPI was greater ($P<0.001$) in the RG-42 than the RG-14 treatment and the treatment \times trial interaction was also significant (Fig. 3A). The greater FCPI by the steers on the RG-42 treatment compared to steers on the RG-14 treatment was primarily caused by the higher crude protein content of their diets 9.4 vs. 8.6%, respectively averaged across the 8 trials (Walker et al. 1989b). The interaction occurred because FCPI was only greater in the RG-42 compared to

RG-14 treatments ($P<0.01$) during the spring and summer trials (i.e., June 1983, March, May, and August 1984) when forage quality was high. The data from the RG-14 and RG-42 treatments were combined into a single RG treatment for further analyses.

RG vs. CG

All variables examined (FOMOUT, OMI, FCPI, and FMEI) were greater ($P<0.001$) for steers in the CG than RG treatment when averaged across dates. FCPI was the only variable that was affected ($P<0.001$) by the interaction of date and grazing treatment. Averaged across dates FOMOUT was 0.6 and 0.7% of body weight in the RG and CG treatments, respectively (Fig. 1B). Within a date FOMOUT only differed ($P<0.02$) between treatments during the January 1983 and March 1984 trials. Averaged across dates OMI was 1.5 and 1.8% of body weight in the RG and CG treatments, respectively (Fig. 1B). Within a date OMI only differed ($P<0.04$) between treatments during the January 1983 and August 1984 trials. FMEI and FCPI followed similar patterns differing ($P<0.01$) only in May and August 1984 when compared within a trial (Figs. 2B and 3B, respectively). A date \times treatment interaction for FCPI was caused by the large difference between treatments at

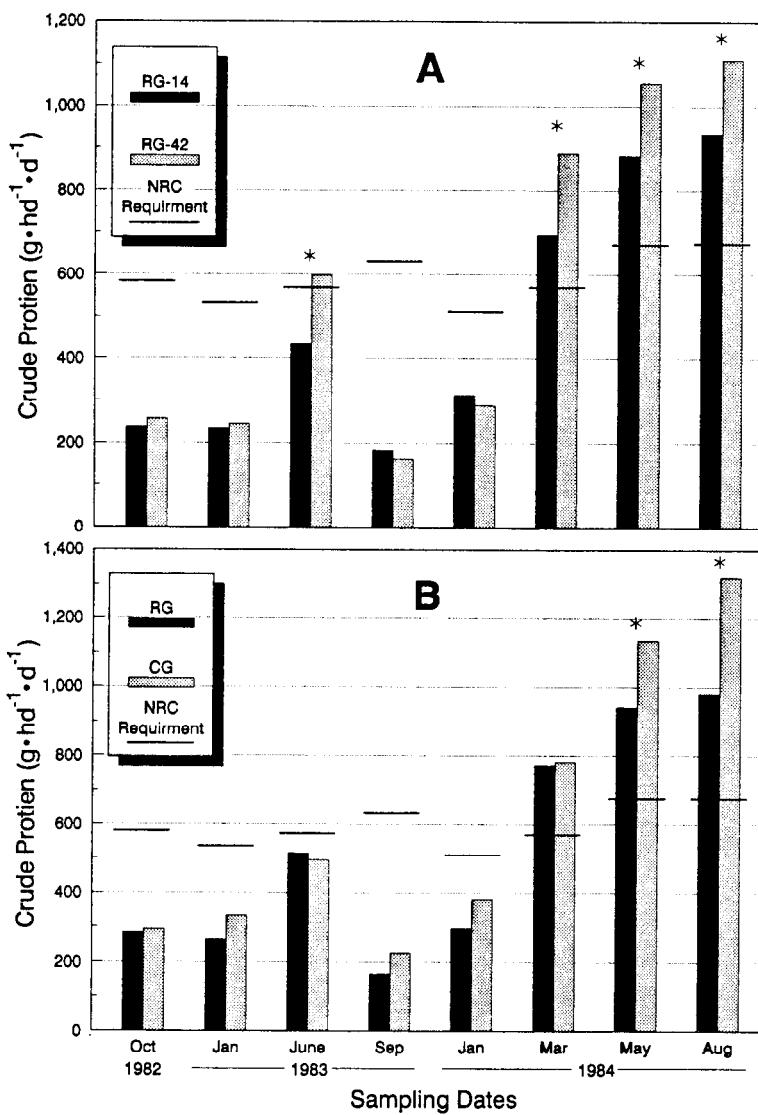


Fig. 3. The effect of livestock density in a rotational grazing treatment (A) or type of grazing treatment (B) on forage crude protein intake on 8 sample dates. Requirements were calculated for each trial using the weight and average daily gain of the steers used to collect nutrient intake data and NRC (1984) recommendations for medium frame steers. Dates with asterisks (*) above them indicate that treatment means are different ($P < 0.05$).

the last 2 dates compared to rather similar levels during the previous trials.

Discussion and Conclusions

The results from this study show that increasing the number of paddocks from 14 to 42 did not enhance nutrient intake. The similarity in forage intake at different livestock densities in the RG treatment (i.e., RG-14 vs. RG-42) agree with previous studies that showed quantity (Heitschmidt et al. 1987a) and quality (Heitschmidt et al. 1987b) of forage, and the quality of diets (Walker et al. 1989b) were also similar between these 2 treatments.

Differences in OMI between the RG and CG treatments appeared to be caused by differences in FOMOUT and/or diet IVDOM that in turn were related to the quantity and quality of available forage. In January 1983 the CG treatment had greater FOMOUT that resulted in higher intake despite lower dietary IVDOM (Fig. 1B). During this trial total herbage standing crop was twice as high in the CG compared to the RG treatment (2100 vs. 1,000 kg · ha⁻¹) (Heitschmidt et al. 1987c). On the other occasion when FOMOUT was significantly greater in the CG compared

to RG treatment (i.e., March 1984) herbage standing crop was again almost twice as high in the CG compared to RG treatment (1400 vs. 700 kg · ha⁻¹). Higher OMI during the August 1984 trial was caused by higher dietary IVDOM in the CG compared to RG treatments. During this trial FOMOUT and total herbage standing crop (Heitschmidt et al. 1987c) were similar between treatments. These data suggest that if differences in forage intake are caused by low forage availability, they will be reflected in a reduction in FOMOUT.

Estimated intakes of ME and CP did not meet NRC (1984) recommendation except for the last 3 trials. Walker et al. (1989c) found that for these data to be used to simulate livestock performance, estimates of both FOMOUT and IVDOM had to be increased. Thus FOMOUT and/or IVDOM were probably under estimated in the first 5 trials.

The results from this and companion studies conducted between 1982 and 1987 provide information explaining why individual animal performance in the RG treatment was consistently less than in the CG treatment. During this period, Heitschmidt et al. (1990) reported that calf weaning weights averaged 260 and 249 kg in the

CG and RG treatments, respectively. The results from this study suggest the reduced performance in the RG treatment was at least a partial result of limited nutrient intake. These limitations appeared to be related primarily to restrictions imposed at various times because of limited amounts of available forage (Heitschmidt et al. 1987c) instead of limitations resulting from reduced diet quality (Walker et al. 1989b). The current findings support those of others who have shown that as forage availability or herbage allowance decreases, nutrient intake (Greenhalgh et al. 1966, Allison and Kothmann 1979, Baker et al. 1981, Parsons et al. 1983) and livestock performance (Hart 1972) also decline regardless of grazing strategy (Olson 1984, Ralphs et al. 1986, Hart et al. 1988). However, when using these same data to simulate animal performance with a deterministic model, Walker et al. (1989c) found that simulated treatment differences in calf weights were greater than actual differences. They suggested that greater frequency of diet sampling by steers in the RG relative to CG treatment may have resulted in an underestimation of FOMOUT by the steers in the RG treatment.

Finally, it should be emphasized that the results from this study do not provide evidence that forage nutrient intake in a properly stocked RG treatment would be different from that in any other properly stocked grazing treatment. The results simply imply that forage nutrient intake will periodically be less in heavily stocked than moderately stocked, yearlong grazing treatments.

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Dependence of standing crop on range condition rating in New Mexico

JAMES A. TIEDEMAN, RELDON BECK, AND ROBIN VANHORN ECRET

Abstract

The Sandy Ridge Site of southern New Mexico was studied to determine the dependence of total standing crop and components of standing crop on range condition rating. Total standing crop which included mesquite (*Prosopis glandulosa* Torr.) decreased, but total standing crop minus mesquite increased as range condition rating increased. These relationships were found to be highly significant ($P \leq 0.01$) by regression analysis. Very low R-square values for these models indicate that the often assumed positive linear relationship of standing crop to range condition rating is not reliable. Prediction of standing crop from range condition ratings using linear or quadratic models was found to be unreliable for the Sandy Range Site in southern New Mexico.

Key Words: ecological status, trend, forage production, biomass

Range condition classification has become the basis for adjusting stocking rates and revising management plans, a procedure which has resulted in considerable controversy. One commonly used procedure, developed by Dyksterhuis (1949), assumes that forage production increases as range condition increases. This study was conducted to determine if this relationship applies to a rangeland area classified and mapped as the Sandy Range Site in southern New Mexico.

With the Dyksterhuis method, rangelands in early stages of secondary succession are classified poor while those in climax stages are excellent. The procedure is based on estimating the percentage of the present plant species composition by aerial cover or weight that is considered to be part of the climax stage of succession for the site.

Four condition classes are:

Poor	0 to 25% of climax
Fair	25 to 50% of climax
Good	50 to 75% of climax
Excellent	75 to 100% of climax

The Range Inventory Standardization Committee (1983) proposes that the term range condition be replaced with ecological status and the classes of poor, fair, good, and excellent be replaced with the classes of early seral, mid seral, late seral, and potential natural community, respectively. The plant species composition in the potential natural community (often called climax) of a "Range Site" is determined by using areas subjected to minimal disturbance that have been excluded from grazing for long periods of time (relic areas).

Many range managers recommend or set lower stocking rates on poor condition range relative to good condition range based upon the assumption that forage production is lower in lower condition classes (Dyksterhuis 1949, USDA 1976). This assumption was supported by Goebel and Cook (1960) in southern Utah. They found that poor condition range had lower forage production with less palatable forage than good condition range. Infiltration rates

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This study was approved by the Director, Washington State University College of Agriculture and Home Economics Research Center, as Scientific Paper 7531, Project 0698, and was supported by the Range Improvement Task Force of New Mexico State University. The authors wish to thank Drs. J.R. Aldredge, G.M. Southward, T.S. Russell, and R.C. Chapman for their assistance and advice in statistical analysis.

Manuscript accepted 11 April 1991.

of water into the soil were also the lowest on the poor condition range. Other studies conflict with this assumption. Cook et al. (1965) found slightly more total forage produced on range in the poor condition class than range in the good condition class.

Smith (1979) found that the method used to rank range by condition classes is inadequate and proposed that it be modified. His assertion was that range condition based on climax composition may not be meaningful in terms of management and that climax or near-climax condition classes may not be as desirable to the land manager's goals as the lower condition classes. For example, on range where sagebrush (*Artemesia tridentata* Nutt.) has been destroyed, forage production is usually higher but condition rating is lower than excellent condition range where sagebrush remains as part of the climax plant community. Modifications to current condition concepts have been suggested by the Range Inventory Standardization Committee (1983). The state-and-transition model (Westoby et al. 1989) is an alternative to the range condition model. It emphasizes management for transition to desired stable states rather than adjustment of stocking rate toward succession along a gradient towards climax as practiced under the range condition model. The objectives of our study were to:

- determine if there is a dependence of various components of standing crop on range condition rating (i.e., if forage production increases as range condition rating increases),
- quantify the amount of change in standing crop for a given change in range condition rating, and
- determine how accurately estimated standing crop can be predicted from range condition rating using a simple linear model (the model most commonly applied).

Study Area

Field sampling was conducted from 18 August to 22 October 1977, on the New Mexico State University's Agricultural Experiment Station Ranch, 20 km north of Las Cruces. The climate is arid with the mean annual precipitation for a 40-year period of 215 mm, most of which falls during the growing season (July, August, and September). June is the warmest month of the year with an average maximum temperature of 34° C. January is the coolest month of the year with an average of 13° C. The precipitation in 1977 during this study period was slightly above normal in August and October, but only 15% of the normal for September (U.S. Department of Commerce 1977).

Data were collected from 2 similar areas, each containing areas varying from poor to good condition. Previously in 1967, one of the areas was fenced into 3 pastures to separate the predominantly good condition range designated pasture 3N, (451 ha); fair condition range, pasture 3W, (668 ha); and poor condition range, pasture 3S, (526 ha). The 3 pastures had been grazed under a seasonal suitability grazing system (Beck 1978). The other area, pasture 15 (1,348 ha), was continuously grazed.

The study area is classified as semidesert grassland with the vegetation varying from homogeneous stands of black grama (*Bouteloua eriopoda* Torr.) to nearly pure stands of mesquite. Extensive sand dunes have developed where mesquite has invaded these sandy soils. The study area is described and mapped as

Methods

One hundred twenty transects were sampled in the study area using ten 0.89-m² quadrats per transect. Fifty six, 24, 20, and 20 transects were randomly located in pastures 15, 3W, 3S, and 3N respectively. Standing crop green weight of each species in a quadrat was estimated in the field according to the methods developed by Pechanec and Pickford (1937) and tested by others as summarized by Cook and Stubbendieck (1986). Standing crop was the total amount of living plant material in aboveground parts, expressed on a per unit area basis at a given point in time. Field personnel were trained by estimating, then clipping and weighing practice plots prior to actual sampling. Estimated plots were occasionally clipped during sampling to verify and if necessary modify estimates. Plants of each species were harvested monthly, weighed green, then air dried each month to develop conversion factors to convert green weights to air-dry weights on a monthly basis. Woody material from previous years' growth was not included in the estimates.

Range condition ratings were determined for each sample transect according to the Dyksterhuis (1949) method as currently used and modified by the SCS (USDA 1976). With this method, the species composition of the potential plant community (Table 1) was compared to the species composition of the plant community of each sample transect. Range condition rating was determined by the summation of the percentage values of species or categories of species common to both plant communities. As described by USDA (1976), the range condition rating is an expression of the relative degree to which the plant species composition of the sample community resembles the presumed climax plant community for the Sandy Range Site. Of the 120 transects, 35, 49, and 36 were classified according to this method as poor, fair, and good condition, respectively.

Regression analysis of 120 sample values was used to determine

the dependence of various components of estimated standing crop (y) on range condition rating (x) for the type of rangeland in southern New Mexico classified and mapped Sandy Range Site.

We evaluated not only total standing crop but also various components of total standing crop because some plant species such as mesquite or broom snakeweed (*Xanthocephalum sarothrae* (Pursh) Shinners) are not useful as forage for livestock in this study area (Rosiere et al. 1975), which directly impacts carrying capacity. The relationship of range condition rating and carrying capacity, was evaluated by comparing range condition rating to (a) total standing crop, (b) total standing crop minus mesquite and (c) components of total standing crop. Components of the total standing crop were total grasses, perennial grasses, annual grasses, perennial forbs, annual forbs, black grama, and a number of individual plant species.

Simple linear models were used to test these relationships. Data transformations and quadratic models were used to further evaluate the dependence of standing crop on range condition rating.

Results and Discussion

Significant linear relationships ($p \leq 0.05$) were determined by regression analysis between various components of standing crop (y) and range condition rating (x). A highly significant negative linear relationship was found between total standing crop and the range condition rating. Although significant, the R-square value (0.43) for the linear model is low, only explaining 43% of the total variation. The quadratic model $y = 965.9 - 28.4x + 0.2x^2$ had a much better fit, explaining 57% of the total variation (Fig. 1).

These data are interpreted as showing that as the composition of climax species increases (i.e., as range condition improves) the total nonwoody standing crop of the Sandy Range Site decreases. However, most of the total standing crop from the poor condition rangeland is from the unpalatable mesquite. The greatest percentage dry weight of the total standing crop is mesquite with an average of 58% for the 120 transects (Table 2).

Table 1. Composition of the potential plant community for the Sandy Range Site. Approximate percentage of total annual herbage yield expressed in air-dry weight (lb) per acre (USDA 1979).

Grasses & grasslike	70-75%	Woody (Shrubs, half shrubs, vines and trees)	10-15%	Forbs	10-15%
Black grama	20-30	Soaptree yucca Longleaf ephedra	5-10	Croton Wild buckwheat Globemallow Euphorbia spp.	3-5
Mesa dropseed Sand dropseed Spike dropseed	15-20	Sand sagebrush Fourwing saltbush Winterfat Broom dalea	1-5	Spectaclepod Desert baileya Filaree	3-5
Bush muhly	5-10				
Plains bristlegrass	1-5	Cacti Broom snakeweed	1-3 1-3		
Arizona cottontop Cane bluestem	5-10			Threadleaf groundsel Desert holly Astragalus spp. Horse nettle Russian thistle Lambquarters Tansymustard	
Tobosa	1-5				1-3
Threeawns	5-10				
Fluffgrass Annual grasses Blue grama	1-5			Other annuals Other perennials	1-5

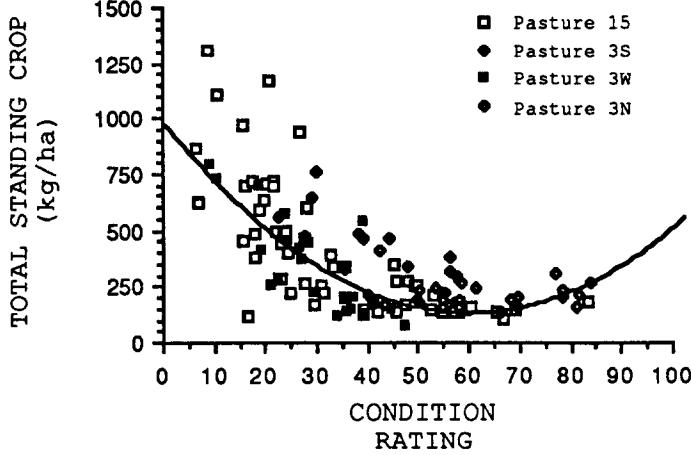


Fig. 1. Total standing crop (kg/ha) in relation to condition rating. Regression curve is best fit quadratic equation: $y = 965.9 - 28.4x + 0.2x^2$, $R^2 = 0.57$, $P \leq 0.01$.

A proper evaluation of range carrying capacity as related to range condition must be directed toward that portion of the vegetation considered useful as forage for livestock or wildlife. A positive rather than negative relationship is found between standing crop and range condition rating when the unpalatable mesquite is eliminated from the total standing crop. Although the regression of total standing crop minus mesquite ($y = 94.9 + 0.9x$) has a significant positive relationship to condition rating, it explains very little, only 8% ($R^2 = 0.08$) of the variation. An extremely low R^2 value implies that y has virtually no linear dependency on x (Lewis-Beck 1986). This relationship is low, negative, or nonsignificant when tested within each pasture.

The relationship of grass standing crop to condition rating was positive ($y = 15.4 + 1.1x$) and significantly correlated ($R^2 = 0.34$) when tested across all pastures. The relationship was either low ($R^2 < 0.16$) or nonsignificant when tested within each pasture except 3N, ($y = -5.2 + 1.5x$, $R^2 = 0.34$), the pasture with the highest mean condition rating (62.6).

The relationship of perennial grass standing crop to condition rating was positive ($y = 17.8 + 1.0x$) and significantly correlated ($R^2 = 0.30$) across all pastures but was low ($R^2 < 0.30$) or nonsignificant when tested within each pasture. Mesa dropseed (*Sporobolus flexuosus* (Thurb.) Rydb.) and black grama had the greatest percent composition by weight of the grass species present (10.4% and 3.5% respectively, Table 2). Separate regression analyses were done on these species. Mesa dropseed had a low but significant correlation ($R^2 = 0.03$) to condition rating. This relationship was not significant across any of the regressions for the separate pastures.

The linear relationship of perennial grass to condition rating was mostly attributed to the black grama standing crop, the second most abundant grass. Black grama had a positive significant correlation ($R^2 = 0.32$) to condition rating with the linear model $y = -13.3 + 0.6x$ but an even better correlation ($R^2 = 0.48$) with the quadratic model: $y = 15.3 - 1.1x + 0.02x^2$. The black grama linear relationship was significant for separate pastures 15 ($y = -7.6 + 0.6x$, $R^2 = 0.28$) and 3N ($y = -64.0 + 1.6x$, $R^2 = 0.43$). This relationship was not analyzed for pastures 3W and 3S, since black grama was present in only 5 transects within these pastures. The relationship of the annual grass portion of standing crop to range condition rating was also low but positive ($y = -2.3 + 0.1x$) and significant ($R^2 = 0.24$). This relationship is not significant for the separate pastures except pasture 3N ($R^2 = 0.20$). Neither total forbs, perennial forbs, nor annual forbs were significantly related to condition rating. The separate analysis of Russian thistle (*Salsola kali* L.), a species contributing the greatest percentage of the annual forb standing

Table 2. Average percent species composition by estimated dry weight for 120 transects, and percent species frequency of occurrence for the Sandy Range Site. Species lower than 0.1% composition are not listed.

Species	% Composition by dry weight	Percent frequency of occurrence in 120 transects
Perennial grasses		
Mesa dropseed (<i>Sporobolus flexuosus</i>)	10.4	91
Black grama (<i>Bouteloua eriopoda</i>)	3.5	39
Fluffgrass (<i>Erioneuron pulchellum</i>)	1.7	75
Spike dropseed (<i>Sporobolus contractus</i>)	1.0	24
Threeawns (<i>Aristida spp.</i>)	0.5	52
Sand dropseed (<i>Sporobolus cryptandrus</i>)	0.2	8
others	0.2	
Total Perennial grasses	17.5	
Annual grasses		
Sixweeks threeawn (<i>Aristida adscensionis</i>)	0.3	23
Needle grama (<i>Bouteloua aristidoides</i>)	0.2	27
Sixweeks grama (<i>Bouteloua barbata</i>)	0.2	33
others	0.1	
Total annual grasses	0.8	
Perennial forbs		
Leatherweed croton (<i>Croton pottsii</i>) var. <i>Pottsii</i>	1.2	57
Wooly paperflower (<i>Psilostrophe tagetina</i>)	1.2	28
Twoleaf senna (<i>Cassia bauhinoides</i>)	0.9	56
Fendler bladderpod (<i>Lesquerella fendleri</i>)	0.4	18
Scarlet globemallow (<i>Sphaeralcea coccinea</i> var. <i>elata</i>)	0.3	24
Silverleaf nightshade (<i>Solanum elaeagnifolium</i>)	0.2	57
Trailing rushpea (<i>Hoffmannseggia incarnata</i>)	0.2	38
Indian rushpea (<i>Hoffmannseggia glauca</i>)	0.2	40
others	0.3	
Total perennial forbs	4.9	
Annual forbs		
Russian thistle (<i>Salsola kali</i>)	4.0	70
Goosefoot (<i>Chenopodium spp.</i>)	1.6	57
Wooly tidesstromia (<i>Tidestromia lanuginosa</i>)	0.4	36
Wislizenius spectacle pod (<i>Dithyrea wislizeni</i>)	0.2	22
Purslane portulaca (<i>Portulaca oleracea</i>)	0.2	14
Rocky Mountain zinnia (<i>Zinnia grandiflora</i>)	0.2	24
others	0.2	74
Total annual forbs	6.8	
Woody species		
Honey mesquite (<i>Prosopis glandulosa</i>)	58.0	74
Broom snakeweed (<i>Xanthocephalum sarotheiae</i>)	4.7	98
Longleaf ephedra (<i>Ephedra trifurca</i>)	3.2	25
Soaptree yucca (<i>Yucca elata</i>)	3.2	73
Fourwing saltbush (<i>Atriplex canescens</i>)	0.4	3
Mescal acacia (<i>Acacia constricta</i>)	0.3	3
Prickly pear cactus (<i>Opuntia spp.</i>)	0.2	4
Total woody species	70.0	

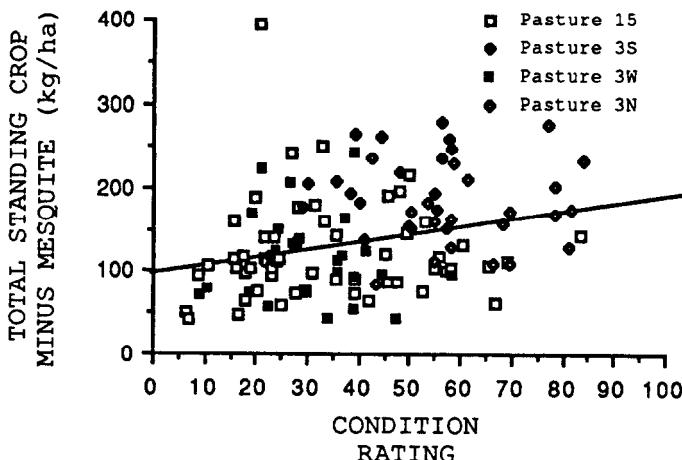


Fig. 2. Total standing crop minus mesquite (kg/ha) to condition rating. Regression curve is the best fit linear equation: $y = 94.9 + R^2 = 0.9x$, $R^2 = 0.08$, $P < 0.01$.

crop, did not show any significant pattern.

In this study where a large number of samples were collected, data were insufficient to reliably quantify a difference in forage production as related to the Dyksterhuis (1949) method of range condition rating. No reliable relationship was found that could be used to quantify increased forage as succession approached climax.

The results of this study are not in conflict with the range manager's goal to improve range condition. A manager could justify low stocking rates on poor condition range on the assumption that low rates are necessary to improve range condition. However, the results of this study do not support the practice of quantifying the difference in total forage production between range condition classes. The amount of forage production from poor condition range at this site is not sufficiently low to justify recommending lower stocking rates.

Dyksterhuis (1949) pointed out that forage production is generally only a reflectance of range condition and was opposed to the view that range condition be measured directly in terms of forage production as proposed by Humphrey (1947). Lower stocking rate recommendations on poorer condition range were simply guides based upon local experiences to bring about rapid improvement in range condition.

Reduction of stocking rate for reasons to improve condition does not appear justifiable for mesquite-infested range in Southern New Mexico. On the nearby Jornada Experimental Range, complete exclusion of livestock on 259 ha since 1933 has not improved range condition, and by 1963, the amount of mesquite cover increased from about 50% to 100% of the area (Buffington and Herbel 1965). On the other hand, reduction of stocking rate for reasons that less forage may be available on poor condition range is justifiable.

Conclusion

We found a positive linear relationship for range condition

rating and total standing crop minus mesquite, and a negative linear relationship for range condition and total standing crop. The 2 relationships are significant and in the direction expected. However, the subject of importance is the current carrying capacity. Neither model is useful for quantifying carrying capacity as reflected in the correlation coefficients for the linear models. Estimated standing crop could not be accurately predicted from range condition ratings. The relationships were found to have more of a quadratic shape than linear.

The method of rating range condition by species composition as most commonly used appears to be reliable for neither assessing range condition as demonstrated by Anderson (1985), nor quantifying carrying capacity as demonstrated in our study for the Sandy Range Site. Revised methods of condition rating need to be developed that are dependable in assessing range condition. If forage production does in fact increase with increased condition, the method should be useful in quantifying carrying capacity.

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Digestibility of guajillo for white-tailed deer

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Abstract

A study was conducted from May 1986 to June 1987 with white-tailed deer (*Odocoileus virginianus*) to determine seasonal nutritive value and nutrient digestibilities of guajillo (*Acacia berlandieri*) and a pelleted diet. In vivo dry matter digestibility (DMD) of guajillo varied seasonally from 35.2 to 48.1% and was inversely correlated to levels of condensed tannins in the forage. Apparent protein digestibility varied seasonally from 13.7 to 45.8% and was a highly dependent function ($R^2 = 0.97$) of the amount of neutral detergent fiber nitrogen (NDFN) digested and the negative impact of condensed tannins. Cellulose and hemicellulose digestibilities also varied seasonally (0.6 to 13.5% and 52.3 to 71.1%, respectively). Nutrient digestibilities of the pelleted diet did not vary by season, sex, or age. Dry matter digestibility of the pelleted diet was $75.6\% \pm 0.9$ and true protein digestibility was $95.0\% \pm 0.04$. Results suggest summer is a stressful period for south Texas deer due to low protein and energy digestibility and high levels of condensed tannins.

Key Words: nutrition, *Odocoileus*, secondary plant compounds, tannins, Texas

South Texas white-tailed deer food habits and feeding preferences are well known (Chamrad and Box 1968, Everitt and Gonzalez 1979, Kie et al. 1980, Varner and Blankenship 1987). The proximate composition and in vitro DMD of deer forages have also been estimated (Varner et al. 1977, Everitt and Gonzalez 1979, Blankenship et al. 1982, Barnes et al. 1990). Relationships between food habits, chemical composition, and in vivo utilization of south Texas deer forages is largely unknown.

Deer in south Texas may consume over 160 plant taxa to meet their nutritional requirements (Chamrad and Box 1968). Forbs are selected whenever available (Kie et al. 1980); however, during much of the year and in drought years especially, the dietary staple of deer is browse (Varner and Blankenship 1987). Browse nutritional value, based on chemical analyses, often is overestimated. This overestimation is often attributed to the presence of condensed tannins, which reduce protein and dry matter digestibilities (Robbins et al. 1987a,b) and interfere with the interpretation of detergent fiber forage analysis (Reed 1986).

There are few data on the ability of deer to make effective use of tannin containing forage. There are also few data describing nutrient digestibility of southern shrubs. Therefore, we initiated this study to (1) gain a more complete understanding of shrub nutritive value, (2) understand the effect condensed tannins have on protein and energy digestion, and (3) complement previous research on food habits, proximate nutrient composition, and in vitro DMD of south Texas shrubs (Varner et al. 1977, Blankenship et al. 1982,

Varner and Blankenship 1987, Barnes et al. 1990). Answers to these questions would allow a more adequate determination of rangeland nutritional carrying capacity for white-tailed deer. Because many ranchers in south Texas feed deer a supplement year round, we also investigated in vivo nutrient digestibilities of a pelleted ration, thus determining the optimum period for supplementation.

Methods

The dietary importance of forage species studied was determined from published studies (Hughes 1982, Varner and Blankenship 1987) and examination of rumen contents of sacrificed deer from Dimmit, LaSalle, Maverick, Uvalde, and Zavala counties, Texas (Varner unpubl. data). Guajillo (*Acacia berlandieri*) is eaten by deer and cattle during all seasons and may constitute up to 37% of the diet (Hughes 1982, Varner and Blankenship 1987).

Guajillo stems, less than 7.0 mm in diameter, were removed by hand clippers from plants growing in shallow soils on the George Lyles Ranch in Zavala and Uvalde counties, Texas. Only current year's growth was collected to resemble deer browsing. This is important because deer usually select live tissue growing on stems less than 2.1 mm in diameter (Shafer 1963). Leaves were stripped from the stem by hand and fed fresh, or stored overnight under refrigeration and fed the following morning. It is important to feed fresh forages since handling affects the quantity of neutral detergent solubles and total phenolic compounds in the vegetation (Servello et al. 1987).

We conducted 5 seasonal, completely randomized balance trials using guajillo during the period June 1986 to April 1987. We also conducted 3 completely randomized balance trials using a pelleted diet (Table 1) during winter, spring, and summer 1986. A trial using

Table 1. Commercially prepared pelleted ration fed to white-tailed deer used in metabolism studies.

Ingredient	Percent composition
Cottonseed meal	29.3
Alfalfa meal	24.2
Corn	19.5
Milo	10.3
Molasses	7.3
Calcium carbonate	2.4
Bentonite	2.4
Dicalcium phosphate	2.4
Sodium chloride	1.0
Auromycin	0.5
Vitamin A	0.25

the pelleted diet was not conducted during the fall because this is not a nutritionally stressful period for deer. Experimental animals were born in captivity, hand-reared on evaporated milk and calf starter, and thereafter maintained on a nutritionally complete pelleted ration supplemented with browse, alfalfa, or native hay, and field corn. A mixture of adult (>2.5 years of age) male and female animals, that were well acclimated to metabolism crates, were used in trials with guajillo because there were no differences in pelleted diet nutrient digestibilities attributed to sex.

Deer (N = 6) were confined in $1.2 \times 1.2 \times 1.2$ m metabolism crates that were housed in a climate-controlled room. Temperatures closely approximated outdoor conditions except in summer,

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Research was supported by the Caesar Kleberg program in Wildlife Ecology at Texas A&M University and the National Rifle Association of America. The assistance of T.J. Fillinger, G.M. Wampler, C. Hensarling, and T.J. VanNorman is appreciated. Appreciation is extended to C.T. Robbins for providing useful information on protein digestibility and A.N. Hagerman for conducting the protein precipitation procedure. D.E. Spangler, F.C. Bryant, J. Reed, and F.A. Servello provided helpful comments on earlier drafts of this manuscript. This is contribution TA239900 of the Texas Agricultural Experiment Station.

Manuscript accepted 20 April 1990.

when daytime temperatures never exceeded 27° C. Animals were weighed prior to each trial, which consisted of a 5-day adjustment period followed by a 5-day total fecal and urine collection period. While 7-day adjustment periods are recommended for reduction of variance in the data (Mothershead et al. 1972), we used a 5-day period because the animals were supplemented with browse prior to each trial, were previously conditioned to the crates, maintained maximal intakes, were not anesthetized, and it was less stressful on the animals. Schneider and Flatt (1975) reviewed the literature and concluded a 5-day pretrial period for cattle was adequate if all that is necessary is to change residual plant materials. They also concluded that longer collection periods result in more precision but may increase bias due "to accident, animal sickness, feed refusal, or other disturbing factors". Holloway et al. (1981), therefore, used a 7-day preliminary trial followed by a 5-day collection period for cattle eating fresh forage. Because deer have significantly faster passage rates than cattle (Huston et al. 1986), a shorter pretrial period should be adequate to remove residual vegetative matter. At worst, a short pretrial period would result in decreased precision and failure to detect the relationships that exist with a decreased possibility of bias (Holloway et al. 1981). Subsequent *in vitro* DMD data were highly correlated with *in vivo* DMD values (Barnes et al. 1989).

Forage was offered *ad libitum* during the pretrial period and fed at maximal consumption levels during the collection period. Deer were fed once in the morning and water was provided *ad libitum* during all experiments.

Forage, orts, and fecal samples were taken daily, oven-dried at 60° C, composited for the total collection period, ground through a 1-mm screen in a Wiley Mill, and subsampled for analyses. Urine was collected daily in opaque plastic containers, acidified with 20% HCL, subsampled, and frozen until analyzed. All samples were analyzed for proximate nutrients, fiber, and gross energy. Gross energy was determined using a Parr adiabatic oxygen bomb calorimeter. All samples were digested following Adler and Wilcox's (1985) perchloric acid and hydrogen peroxide technique (modified by Gallagher, personal communication). Crude protein ($N \times 6.25$) was determined colorimetrically on the wet-digested samples (Laubner 1975). Condensed tannins were extracted in methanol and measured colorimetrically using a catechin standard (Burns 1971). Precipitable protein (cm^2/mg), due to the effects of condensed tannins, was also measured (Hagerman 1987).

Forage and feces were analyzed using detergent analyses (Goering and Van Soest 1970) without the addition of sodium sulfite (Mould and Robbins 1981). Lignin was determined by sequential treatments of acid detergent fiber (ADF) with potassium permanganate. Cellulose and hemicellulose were determined by difference. Nitrogen (Laubner 1975) in NDF of feed and feces was also measured.

Digestible energy (kcal/g) was calculated by multiplying gross

Table 2. Mean body weight (BW) and dry matter intakes (DMI) of white-tailed deer used in metabolism studies.

Diet	N	Weight (kg)	SE	DMI/kgBW	SE
Guajillo Spring	5	43.7	2.1	11.7A ¹	1.4
Early summer	5	49.3	2.4	13.0A	1.9
Late summer	5	30.5	1.0	19.6B	2.5
Fall	6	36.8	1.0	13.3A	1.8
Winter	5	41.1	2.0	20.0B	1.5
Pelleted	7 (A) ²	43.7	1.3	21.0	0.6
	4 (Y)	25.1	0.7	32.4	1.3

¹Values within a column followed by different letters are different ($P \leq 0.05$).

²Indicates a difference ($P \geq 0.05$) in DMI/kgBW between adult (A) and yearling (Y) white-tailed deer.

energy intake \times apparent digestibility. Expected digestible protein in feed was calculated using the equation $Y = -3.87 + 0.9387X$ based on nonphenolic-containing forages fed to deer (Robbins et al. 1987a). Observed digestible protein was calculated by multiplying CP intake \times apparent digestibility (Robbins et al. 1987a). Protein reduction was calculated as the difference between expected and observed digestible protein. True protein digestibility of the pelleted diet was calculated using a metabolic fecal nitrogen value of 4.88 g/100 g feed (Robbins et al. 1974). This source of endogenous nitrogen was removed from digestibility equations.

True protein digestibility of guajillo was estimated by replacing total nitrogen in the feces with fecal nitrogen insoluble in neutral detergent (Mason 1969, Van Soest 1967) because fecal nitrogen that is insoluble in neutral detergent originates from indigestible feed nitrogen; whereas, fecal nitrogen that is soluble in neutral detergent is from microbial and endogenous sources of nitrogen in the digestive tract. A Lucas test (Van Soest 1982) was not used to predict true protein digestibility because the use of regression equations from a Lucas test for uniformity of protein is invalid when applied to feeds that contain tannins (Reed et al. 1990).

Unbalanced one-way analysis of variance and the least significant differences mean comparison tests were used to detect differences in browse nutrient digestibilities. Analysis of variance was also used to determine differences in nutrient digestibilities between pelleted ration trials. A Student's *t* test was used to detect differences in dry matter intake (DMI) and nutrient digestibilities of the pelleted ration by yearling and adult deer. Significance is indicated at the 0.05 level of probability.

Results and Discussion

One individual deer during each trial, except during fall, went off feed and had to be removed from the metabolism crate (Table 2). Mean deer weight (39.4 kg) was not different between trials (Table 2). Deer consumed significantly less guajillo during the spring, early summer, and fall periods and DMI/kg body weight (BW)/day

Table 3. Protein, energy, and neutral detergent fiber (NDF) composition (100% dry matter basis) of forages fed to south Texas white-tailed deer in digestion studies.

Diet	Crude protein (%)	Digestible protein (g/100g feed)	Protein precipitation (cm ² /mg)	Digestible energy (kcal/g)	Condensed tannins (mg/g)	NDF (%)	Cellulose (%)	Hemi-cellulose (%)	Lignin (%)	NDFN (% of total N)
Guajillo spring	20.0	9.14	0.220	2.27	92.1	57.4	15.9	30.4	11.9	49.4
Early summer	20.2	7.31	0.161	1.91	89.9	50.9	16.8	24.4	10.8	46.2
Late summer	15.6	2.14	0.228	1.60	112.8	50.8	18.5	20.0	11.9	52.8
Fall	16.8	3.51	0.206	1.75	108.1	53.8	18.9	24.6	10.4	52.7
Winter	17.6	4.01	0.196	1.93	117.9	59.2	20.1	25.7	12.8	54.0

Table 4. Mean digestibility coefficients (% of dry matter) of forages fed to south Texas white-tailed deer used in metabolism studies.

Diet	Dry matter		Energy		Apparent protein		True protein		NDF	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Guajillo spring	48.1C ¹	0.8	46.0C	0.9	45.8B	2.2	56.8D	0.9	22.8B	1.8
Early summer	41.2AB	2.7	39.1B	2.8	35.5B	4.1	51.1CD	2.3	7.6A	4.5
Late summer	35.2A	2.4	32.5A	2.7	13.7A	3.5	38.0A	2.3	0.0A	3.5
Fall	38.3AB	2.3	35.9AB	2.3	20.5A	5.2	43.0AB	1.8	6.7A	3.1
Winter	41.5D	0.6	38.6AB	0.7	22.7A	2.5	46.6BC	1.6	17.9B	1.2

Diet	Cellulose		Hemicellulose		NDFN		Condensed tannins	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Guajillo spring	0.6A	3.6	71.1C	1.9	34.5B	2.4	92.7C	0.4
Early summer	6.5AB	3.2	65.6BC	3.2	26.2B	5.1	84.8A	0.7
Late summer	11.1B	4.3	52.3A	3.5	14.5A	2.4	82.6A	1.4
Fall	5.9AB	3.2	62.1B	2.5	17.1A	3.1	84.2A	1.1
Winter	13.5B	1.4	67.9BC	1.6	16.8A	1.3	88.4B	0.8

of adult deer consuming guajillo averaged 15.5 g/kg BW/day. Yearling deer, consuming the pelleted ration, had significantly higher DMI/kg BW/day than adults (Table 2). Differences in voluntary intake were expected and are determined by a range of behavioral, morphological, and physiological mechanisms linked to photoperiod and endocrine changes (Allison 1985). Intake levels reported in our study are similar to levels reported in previous studies using mule deer (*Odocoileus hemionus*) or white-tailed deer (Baker and Hobbs 1987, Mautz et al. 1976).

No statistical seasonal comparisons of forage quality could be made because daily feed samples were taken for each deer from a common forage supply and composited for analysis. Gross energy of guajillo was similar and averaged 4.7 ± 0.87 kcal/g (Table 3). Digestible energy (DE) averaged 1.89 kcal/g and varied seasonally. Dry matter digestibility of guajillo varied seasonally and averaged 40.8% (Table 3). Condensed tannins were inversely correlated to DMD ($Y = 63.1 - 0.2X$, $R^2 = 0.60$) but not to NDF digestibility ($Y = 32.2 - 0.2X$, $R^2 = 0.20$). The lack of relationship between condensed tannins and NDF digestibility is not surprising because condensed tannins appear to elevate NDF content as a result of insoluble complexes being formed with protein and carbohydrates (Reed 1986).

Dry matter digestibility is an important nutritional variable to measure since it provides a strong and direct inference to energy utilization within the animal (Barnes et al. 1989). White-tailed deer have been classified as concentrate selectors (Hanley 1982) which dictates energy should come from fermentation of cell solubles. These solubles should be 100% digestible (Van Soest 1982) unless phenolics or volatile oils are present. We observed a reduction of 18 to 34% (from theoretical limit of 98 to 100% digestible) in the digestibility of cell solubles. The inverse relationship between DMD and concentration of condensed tannins and reduction in theoretical digestible cell solubles indicate condensed tannins exert their primary influence through reducing digestible cell solubles (Robbins et al. 1987b) and not by reducing cell wall digestibility (Barry and Manley 1984, Barry et al. 1986). However, without quantifying changes in condensed tannin solubilities and their effects on fiber analysis, it is difficult to pinpoint cause and effect (Reed 1986) especially since condensed tannins can complex with protein to elevate NDFN (Reed and Soller 1987), a substantial proportion of NDF.

Cellulose digestibilities were low (0.6–13.5%) for guajillo and were lowest during the spring (Table 4). Hemicellulose digestibility

varied seasonally and averaged 63.7%. Hemicellulose digestibility was lowest during late summer. The highly variable and low digestibility of cell wall fractions may be attributed to insoluble complexes formed with condensed tannins which interfere with the detergent analysis system (Reed 1986).

Digestion of cell wall components, especially if highly lignified (mean lignin content of guajillo was $11.6 \pm 0.17\%$), is a slow process. Fiber available for conversion into energy are cellulose and hemicellulose with the upper digestion limit set by lignin, cutin, and silica content. Because tannins appear to form insoluble protein and carbohydrate complexes, NDF may not be an accurate measure of cell wall in browse (Reed 1986). However, our data indicate that hemicellulose is digested more easily by deer than is cellulose or that the microbial population was better adapted for digesting hemicellulose (52.3–71.1% digestible) than cellulose (0.6–13.5% digestible) which is consistent with predictions for a concentrate selector (Kay et al. 1980). Passage rate ultimately determines fiber digestion (Huston et al. 1986). These factors (passage rate, low cellulose digestion, and tannin formed insoluble complexes) might have accounted for the low DMD of guajillo during the late summer and fall periods especially since passage rate of guajillo is fastest during the late summer period (Barnes et al. 1991).

Digestibility of condensed tannins varied seasonally (Table 4) and was higher than expected. These high digestibilities may be attributed to minimal recovery of condensed tannins in the feces because they had complexed with protein and carbohydrates upon passage through the digestive tract and were no longer soluble (Reed and Soller 1987).

The CP of guajillo was highest during periods of active growth in the spring and early summer, declined in late summer, then increased in response to new growth in the fall (Table 3). A substantial portion of total nitrogen was bound to NDF (range 46.2 to 54.0%, $\bar{x} = 50.3\%$). There was no significant relationship between digestible protein reduction and protein precipitation measured using the ring diameter squared method (Table 3). Availability of apparently digestible protein in the browse diets was reduced from expected digestible protein of nonphenolic containing forages (Robbins et al. 1987a) by 3.5 to 8.5%. Digestible protein reduction was highly correlated to condensed tannin concentration in the diet ($Y = -2.4 + 0.1X$, $R^2 = 0.86$). Reed et al. (1990) observed a theoretical reduction in protein availability of 35% (compared to an average of 88% in nontannin containing uniform feeds (Van Soest

1982)) in a tanniniferous *Acacia*. They suggested lower apparent and true protein digestibility was related to a high excretion of fecal NDFN. The high excretion of fecal NDFN could be attributed to the presence of phenols which complex with protein and caused an increase in apparent lignin content of the feces, leading to negative digestibility of lignin and NDFN (Reed 1986).

True protein digestibility varied seasonally and is considerably lower than true protein digestibility of uniform feeds (approximately 88%, Van Soest 1982) such as the pelleted diet (95.0%). This lowered digestibility can be attributed to the presence of phenolics (Reed et al. 1990) that reduce protein availability (Robbins et al. 1987a) and cause the nitrogen to form insoluble complexes with fiber (Reed 1986). These complexes result in elevated fecal NDFN digestibility coefficients. Reed and Soller (1987) observe that phenolics increase the amount of endogenous nitrogen, including urea, recycled to the rumen which increased microbial utilization of endogenous nitrogen.

Digestible or available protein, not CP content of the forage, is the nutritionally important factor in meeting animal requirements. Available protein is a function of the total amount of CP present minus the indigestible NDFN and the extent of protein precipitation by tannins (Robbins et al. 1987a). A large part of the variability in protein digestibility of guajillo appears related to the presence of condensed tannins. Digestible protein reduction (compared to expected digestible protein in nonphenolic forages) of 3.5 to 8.5% in the browse diets agrees with values obtained by Robbins et al. (1987a). Deer may be able to avoid these effects behaviorally by selection of older, less toxic stems (Provenza and Malechek 1984), increasing DMI, or selection of nonphenolic forages (Bryant and Kuropat 1980). Nonphenolic forages are often scarce in south Texas during the summer or extended periods of drought. Deer may also minimize nitrogen loss by complexing tannin with salivary glycoprotein (Austin et al. 1989).

The remaining variability in apparent digestible protein of guajillo is a result of the amount of NDFN in the forage and NDFN digestibility. This source of nitrogen becomes available only if NDF can be digested. Small quantities of NDF and subsequently small amounts of NDFN were digested by deer in this study. However, condensed tannins can interfere with fiber analysis by forming insoluble complexes (Reed 1986) and NDF and NDFN digestibility may be greater than reported. The CP content of the browse rations were well above the 6 to 8% required for minimal ruminal function, but available protein became low as the forages matured and tannin levels increased. Protein precipitation during the late summer and fall periods was exacerbated due to low quantities of NDFN being digested, which may be a function of rapid passage of fiber particles (Barnes et al. 1991) or tannin-protein complexes (Reed 1986, Reed et al. 1990).

There were no seasonal differences in nutrient digestibility between pelleted diet trials. Consequently, data were pooled and tested for differences attributed to age and sex. There were no digestibility differences attributed to age or sex, consequently data were pooled. Gross energy of the pelleted diet was 3.8 kcal/g, whereas digestible energy was 2.96 kcal/g. Dry matter digestibility of this diet was $75.6 \pm 0.9\%$. Neutral detergent fiber, cellulose, and hemicellulose digestibilities were 81.7 ± 0.7 , 62.0 ± 1.6 , and 93.5 ± 0.5 , respectively. This diet is an excellent source of energy. The pelleted diet contained 22.5% CP and had 21.62 g/100 g feed digestible protein. True protein digestibility of this diet was $95.0 \pm 0.04\%$. The true protein digestibility of this diet is in close agreement with that found in other studies indicating deer are not different from domestic ruminants in their ability to digest protein in nonphenolic forages (Robbins et al. 1974).

Our information indicates white-tailed deer meet their relatively high weight specific metabolic requirements through digestion of

neutral detergent solubles, consistent with current ecological foraging theory of small ungulates. Late summer is the most stressful nutritional period for deer in south Texas due to low DMD, DE, and digestible protein in browse, which is a function of increased condensed tannins and low NDF digestibilities. This is the period when supplementation with the pelleted ration could have its greatest impact because this diet was highly digestible, containing approximately 3 kcal/g DE, and 21 g/100 g digestible protein. The nutritional value of any forage should not be explained using a 1-dimensional approach such as proximate analyses, digestibility, rate of digestion and passage, or phenolic content. More research on the effects condensed tannins have on protein metabolism, rumen microorganisms, and ruminant digestive enzymes is needed to better predict the nutritive value of forages containing secondary plant compounds. We present information that indicates complex relationships exist between intake, nutrient digestibilities, and secondary plant compounds.

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Bias in aging feral horses

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Abstract

Several investigators studying feral horses (*Equus caballus*) in the western U.S. have noted anomalies in the age distribution of captured horses that raised concern about the accuracy of aging technique. Possible biases in the aging technique were investigated by assembling records for 60,116 horses removed from public lands in Nevada, Oregon, and Wyoming between 1975 and 1987. Records were consolidated for each state and the resulting age distributions were compared to an expected distribution derived from a population model based on published demographic parameters. These comparisons revealed a tendency for 5-year-olds to be under represented while 6- and 7-year-olds were over represented. There were also higher than expected numbers of horses aged as 15 and 20 years. These apparent anomalies were consistent among states and also among years within each state. The pervasiveness of the trends demonstrates that several biases exist in the current aging technique. Given these uncertainties, it is recommended that development of age-specific demographic variables based on yearly increments beyond age 3 or 4 be avoided, instead lumping data into broad age classes whenever possible.

Key Words: age structure, aging techniques, demography, *Equus caballus*

Controversy about management of feral horses (*Equus caballus*) occupying public lands in the western United States has stimulated studies of many demographic parameters based on age-specific data (National Research Council 1980, Wolfe 1980, Seal and Plotka 1983, Berger 1986, Siniff et al. 1986, Plotka et al. 1988, Garrott and Taylor 1990). Two of these studies reported data on age structure (National Research Council 1980, Wolfe 1980) and both detected anomalies that raised concern about the accuracy of age estimates (National Research Council 1982). Techniques for estimating age of animals may be subject to random error (measurement and sampling), systematic bias, or a combination of both. Depending on how age data are used, such errors can have significant affects on estimation of demographic parameters (Cooke and de la Mare 1983, de la Mare and Cooke 1984), hence, careful evaluation of aging techniques is important.

Accuracy of aging techniques cannot be assessed without known-age animals (Dapson 1980); however, if age distributions are similar among populations, systematic biases may be detected by aging a large number of animals and examining the resulting age distributions (Fatti et al. 1980). Garrott et al. (1991b) reported similar demographic characteristics and growth rates for a variety of feral horse populations throughout the western United States, suggesting examination of age distributions may be useful for assessing possible bias in techniques used to estimate age of feral horses. The objective of this paper is to present the results of such a study using age distribution derived from horses captured by the Bureau of Land Management (BLM) over a 12-year period.

Methods

Records for 60,116 horses removed from public lands between 1975 and 1987 were obtained from BLM offices in Nevada,

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Funding was provided by BLM contract USDI-AA852-CT5-29. The author wishes to thank D.B. Siniff, J.R. Tester, A.M. Starfield, and T.C. Eagle for assistance and editorial suggestions and the many BLM employees who provided data.

Manuscript accepted 6 April 1991.

Oregon, and Wyoming. Animals were captured using helicopters to locate and herd bands of horses into corral traps. Captured horses were transported to centralized processing facilities in each state. Each animal was restrained in a padded squeeze chute and aged by veterinarians or experienced BLM personnel using standardized dental criteria (Amer. Assoc. Equine Practitioners 1981). Eruption sequences of incisors were used to determine age through 5 years, when the last permanent incisors are fully erupted. Estimating ages beyond 5 years was more subjective because it relied on various characteristics of tooth wear and form. Horses were aged to the nearest year except in Wyoming, where no attempt was made to estimate the age of animals ≥ 12 years old.

In order to assess possible aging bias, I compared the age distributions constructed from the data to an expected distribution derived from the demographic studies of Garrott et al. (1991b), Eberhardt et al. (1982) and Garrott et al. (1991b) provide evidence that many feral horse populations were growing at a relatively constant rate during the period when the age data were collected. The results suggest that survival and fecundity also remained relatively uniform, which would result in a stationary age structure (Caughley 1977). Garrott et al. (1991b) developed age-specific survival and fecundity schedules using the equations of Siler (1979) and Eberhardt (1985) and several sources of data. These schedules were combined in a variant of a Leslie matrix population model described by Garrott (1991) to calculate the stable age distributions (Starfield and Bleloch 1986). Age distributions were calculated for all 16 combinations of the 4 survival and 4 fecundity schedules presented by Garrott et al. (1991b). Of the 8 schedules presented by Garrott et al. (1991b), only the S1 survival schedule and the F1 and F2 fecundity schedules were developed from data. For the purpose of generating an expected age distribution for comparison with the observed age distributions presented in this paper, I chose to use the S1 survival and F2 fecundity schedules because they represent the most extensive data yet published. The S1 schedule was produced from survival data where all horses in a small Montana population were individually known and their fate followed for an 11-year period (Garrott and Taylor 1990). The F2 fecundity schedule was developed from the lactation status of 1,144 mares captured in June during 3 consecutive years from a herd in Nevada (Garrott et al. 1991a).

Statistical comparisons between the observed and expected age distributions were made by constructing a 2 by 11 contingency table for each state. Only the first 11 age classes (0–10 years) were used in the tests in order to reduce the influence of sampling variation due to the relatively small number of horses assigned to older age classes. The chi-square statistic was used to test for departures from the expected age distribution.

Results

Age distributions from all 3 states had a variety of peaks and troughs that deviated from the expected smooth distribution (Table 1). With the exception of an apparent under representation of yearlings in data from Oregon, number of horses assigned to each age class from foal to 5 years steadily decreased, as expected. Because the low proportion of yearlings was unique to data from Oregon, it cannot be attributed to aging criteria, but must represent a problem peculiar to that state.

At 5 years of age when the aging criteria switch from incisor

Table 1. The age distribution of feral horses removed from public lands in Nevada, Oregon, and Wyoming between 1975 and 1987 and the expected stable age distribution derived from the S1 survival and F2 fecundity schedules presented by Garrott et al. (1991).

Age (yr)	Expected Percent	Observed					
		Nevada		Oregon		Wyoming	
		N	Percent	N	Percent	N	Percent
0	19.95	5993**	17.88	1881**	20.27	2948**	17.03
1	15.44	5092	15.19	960	10.34	2747	15.87
2	12.52	4140	12.35	1393	15.01	2614	15.10
3	10.16	3096	9.24	928	10.00	1559	9.00
4	8.24	2485	7.41	741	7.98	1495	8.63
5	6.69	1806	5.39	504	5.43	646	3.73
6	5.42	3098	9.24	765	8.24	759	4.38
7	4.39	2325	6.94	598	6.44	914	5.28
8	3.56	1375	4.10	389	4.19	802	4.63
9	2.88	558	1.66	213	2.30	536	3.10
10	2.33	514	1.53	284	3.06	393	2.27
11	1.88	251	0.75	203	2.19	375	2.17
12	1.52	493	1.47	82	0.88		
13	1.22	452	1.35	16	0.17		
14	0.97	203	0.61	56	0.60		
15	0.77	343	1.02	113	1.22		
16	0.61	116	0.35	16	0.17		
17	0.47	136	0.41	2	0.02		
18	0.35	160	0.48	10	0.11		
19	0.25	31	0.09	33	0.36		
20	0.17	483	1.44	80	0.86		
21	0.10	31	0.09	0	0.00		
22	0.05	39	0.12	1	0.01		
23	0.02	41	0.12	1	0.01		
24	0.01	57	0.17	4	0.04		
25	0.00	79	0.24	6	0.06		
>25		106	0.32	2	0.02		
Total		33521		9281		17314	

**Tests of expected vs. observed distribution for ages 0–10 within each state significant at the 0.01 level.

eruption to wear characteristics, age structures from all 3 states deviate from the expected smooth distribution, with the proportion of horses classified as 6- and 7-year-olds exceeding the proportion classified as 5-year-olds (Table 1). Deviations from the expected age distribution in the 5–7 year age classes were responsible for 50 to 78% of the overall chi-square statistic for each state. If these anomalies were the result of abnormally high recruitment for several years throughout western populations, then the strong cohorts should move through the population with time. Examination of the age distributions of horses captured in consecutive years, however, demonstrates that the peak in 6–7 year olds remained stationary (Fig. 1), suggesting a systematic bias in the aging technique.

The age distributions beyond 9 years old are erratic and show a strong bias toward multiples of 5. This bias is particularly noticeable for the 15- and 20-year age classes, but is also evident to a lesser extent in the 10- and 25-year age classes (Table 1).

Discussion

The National Research Council (1980) noted under representation of yearlings in age distributions of horses derived primarily from Oregon BLM data and attributed the problem to sampling bias (i.e., yearlings were not captured in proportion to their availability). This explanation seems questionable for 2 reasons. First, all 3 states used similar techniques for capturing horses; therefore, any sampling bias associated with the capture technique should also be present in data from Nevada and Wyoming. Second, yearlings are not spatially or socially segregated in horse populations, but usually are associated with harems or bands of stallions (Berger 1986). The normal procedure when capturing horses was to consolidate several of these social groups and herd them as a unit into a corral

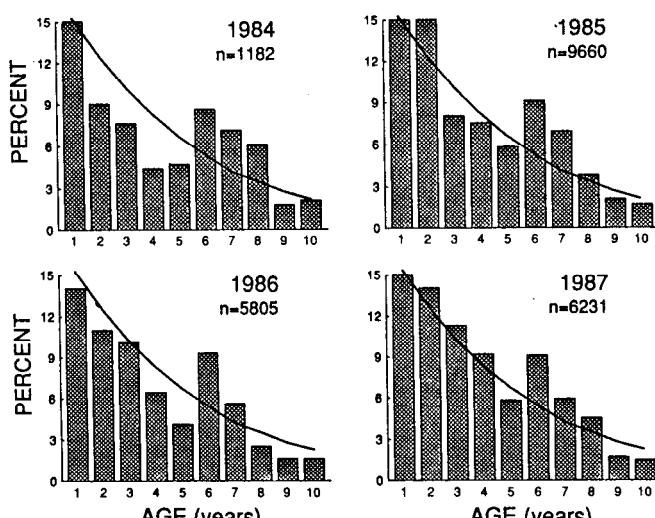


Fig. 1. Age distributions of feral horses removed from public lands in Nevada during 4 consecutive years. The line represents the expected stable age distribution derived from the S1 survival and F2 fecundity schedules presented by Garrott et al. (1991).

trap. Thus, there was no obvious mechanism that would make yearlings less susceptible to capture.

An alternative explanation for the deficiency of yearlings in these Oregon data is the systematic misclassification of yearlings into adjacent age classes. Discussions with Oregon BLM personnel revealed that horses were considered yearlings if the third deciduous incisors were partially erupted, but if these incisors were fully

erupted and in contact with opposing teeth, the animal was considered a 2-year-old. The third incisors, however, are in contact by 18–20 months of age (Ensminger 1977, Amer. Assoc. Equine Practitioners 1981). Hence, yearlings aged in late autumn or winter, the primary capture period, may have been misclassified as 2-year-olds. This supposition is supported by the large 2-year-old cohort in the Oregon data.

The most reasonable explanation for the preponderance of horses assigned into the 6- and 7-year age groups is the misclassification of animals from adjacent age classes into the 6- and 7-year age groups. Caughey (1965, 1977) demonstrated considerable variation in the timing of tooth eruption and wear patterns between individual Himalayan thar (*Hemitragus jemlahicus*). Similar variation probably exists in other large herbivores as well. This variation would result in errors in estimating age of animals that can best be visualized as a probability distribution. An animal that is X years old may have a 0.50 probability of being assigned into the correct age class based on dental characteristics, a 0.20 probability of being assigned into either the X-1 or X+1 age classes, and a 0.05 probability of being assigned into either the X-2 or X+2 age classes. For example, some 5-year-old animals will have greater than normal incisor wear and be classified as 6-year-olds, whereas, incisors of some 6-year-olds will have less than normal wear and be classified as 5-year-olds. These errors obviously are not compensating in the first several age classes that use incisor wear to estimate age. There is a tendency for 4- and 5-year-old age classes to be under represented in the data when compared to the expected distribution (Table 1, Fig. 1), suggesting these animals may be the source for the overabundance of 6- and 7-year olds. The reason for this is uncertain, but it is clear from data in Table 1 and Figure 1 that aging errors were common and a distinct bias exists in these age classes.

The American Association of Equine Practitioners (1981) cautions that after all permanent teeth are fully erupted, aging becomes increasing difficult and Ensminger (1977) states that horses cannot be accurately aged beyond 12 years. The age distributions from both Nevada and Oregon, where horses were assigned ages up to 30 years, provides evidence that aging older animals is quite speculative.

Given the uncertainties of the current aging criteria, caution should be exercised when developing age-specific demographic variables based on incisor eruption and wear. With the exception of the yearling age class in Oregon, no consistent biases were detected in the 0- to 4-year age classes, therefore, development of survival and fecundity rates based on yearly increments appears reasonable. These age classes are of particular significance in assessing age of first reproduction, since this is an important parameter in population models of long-lived mammals (Eberhardt 1985). Results of this study suggests that beyond age 4 it would be judicious to group horses into broader age classes such as 5–9, 10–14, 15–19, and ≥20. Such general age classes would not adversely affect the development of age-specific survival and

fecundity schedules because both survival and fecundity of large mammals remains relatively constant after animals become mature until the onset of senescence in the oldest age classes (Eberhardt 1985). Future research on estimating ages of feral horses that could be useful would include comparing age estimates based on tooth eruption and wear with known-age animals and ages based on tooth cementum structures.

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Instantaneous intake rates of 9 browse species by white-tailed deer

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Abstract

Instantaneous intake rate (IIR) and instantaneous nutrient intake rate (INIR) by tame white-tailed deer (*Odocoileus virginianus*) of 9 common browse species in south Texas were studied to determine if morphological properties of the plants were associated with intake rate, and if IIR and INIR correlated to preference ratings derived from percent time spent foraging a particular species and with total foliage consumed. Mean leaf mass showed a significant ($P<0.05$) positive correlation to IIR ($r=0.75$), INIR of neutral detergent fiber ($r=0.73$), acid detergent fiber ($r=0.73$), and acid detergent fiber nitrogen ($r=0.68$). Mean leaf length showed a significant ($P<0.05$) positive correlation to INIR of crude protein ($r=0.67$). Thorn density showed no significant ($P>0.05$) correlations to IIR or INIR. Leaf weight/stem weight ratio showed a significant ($P<0.05$) positive correlation to IIR ($r=0.65$) and INIR of acid detergent fiber nitrogen ($r=0.81$). Rankings of IIR and INIR did not agree with preference indices based on weight of forage removed or amount of time spent browsing. Significant ($P<0.05$) positive correlations for all trials between preference indices based on weight removal and time spent browsing ($r=0.73$ for new leaf development, $r=0.87$ for stem elongation, and $r=0.70$ for full leaf development) indicated these 2 techniques closely agreed on species rank.

Key Words: instantaneous intake rate, instantaneous nutrient intake rate, white-tailed deer, *Odocoileus virginianus*, browse

Browse is a major component of white-tailed deer (*Odocoileus virginianus*) diets in subtropical thornscrub woodlands in south Texas and northern Mexico. Although diet selection can vary between herds and with season (Arnold and Drawe 1979), numerous species of browse plants have been found to consistently make up a large part of deer diets in this area and several have been termed as preferred food plants (Davis 1952, Davis and Winkler 1968, Chamrad and Box 1968, Drawe 1968, Everitt and Drawe 1974, Arnold and Drawe 1979). Preferential selection for a species is hypothesized as being correlated with palatability as well as with availability (Willms 1978). Palatability has been defined as a plant characteristic that stimulates a selective response by foraging animals (Heady 1964) and may determine the duration of foraging and ingestion rate. Profitability of browsing should be directly and positively related to the amount of nutrients an animal can consume in a given time.

Morphological attributes of plants, including growth form, biomass of leaves, and presence of thorns or other forms of spinescence, may interact to defend foliage loss to herbivory (Willms 1978, Cooper and Owen-Smith 1986). While most browse plants in south Texas are armed with spines or thorns, many are considered important foods for white-tailed deer. Free-ranging herbivores select diets from plants that differ in canopy shape and architecture as well as temporal and spatial variation (Provenza and Ralph 1990). More controlled environments are needed to differentiate individual plant parameters affecting intake rate. Our objectives were to determine if morphological properties of browse plants

were associated with instantaneous intake rate (IIR) and instantaneous nutrient intake rate (INIR) by deer, and if IIR and INIR correlated to preference rankings by percent time spent foraging on a particular species and with amount of foliage consumed.

Study Area and Methods

The study was conducted on the Texas Agricultural Experiment Station's La Copita Research Area ($27^{\circ} 40' N$, $98^{\circ} 12' W$) about 15 km southwest of Alice, Texas, in Jim Wells County. Vegetation of La Copita is characteristic of the northern Tamaulipan thornscrub woodland. The climate is subtropical with hot, humid summers and mild winters with an average growing season of >260 days. Long-term mean precipitation is 716 mm with maxima in May–June and September (Scifres and Koerth 1987).

Deer used in the trials were 3 male and 1 female yearlings (1 yr old at Trial 1). All deer were tame and readily accepted hand feeding. Deer were held in a 0.2-ha pen containing some native woody and herbaceous plants but primarily maintained on a commercially available pelleted feed. While in the holding pen, all deer were introduced to hand feeding of cut branches of the various plant species. The deer also were trained to feed from branches stapled to sawhorses used in our preference trials. Habituation was started as soon as the deer were completely weaned from bottle feeding as learning and experience early in life may influence preferences or aversions and enables young animals to acquire necessary skills to efficiently harvest different forages (Provenza and Ralph 1988). McMahan (1964) felt that feeding behavior and plant selection by experienced tame white-tailed deer were similar to those of their wild counterparts.

Instantaneous Intake

To estimate IIR, 9 browse species known to be eaten by white-tailed deer in south Texas (Everitt and Drawe 1974, Arnold and Drawe 1979) were used and included guajillo (*Acacia berlandieri* Benth.), huisache (*A. farnesiana* (L.) Willd.), blackbrush (*A. rigidula* Benth.), Texas persimmon (*Diospyros texana* Scheele), spiny hackberry (*Celtis pallida* Torr.), brasilia (*Condalia obovata* Hook.), coma (*Bumelia celastrina* H.B.K.), lime pricklyash (*Zanthoxylum fagara* (L.) Sarg.), and kidneywood (*Eysenhardtia texana* Scheele). For the instantaneous intake trials the deer were confined in an 8 × 5-m pen divided into 2 sections. Individual deer could be penned in 1 section for feeding. Five branches (terminal 50 cm) of each browse species were offered separately to each of 4 deer for 30 sec during each trial. Branches were held in a horizontal position about 0.5 m above the ground. Branches were selected from plants growing adjacent to the holding pen to minimize weight loss through desiccation. Branches were weighed to the nearest 0.01 g immediately before and after offering to determine intake. Branches were of sufficient size so that no more than a mean of about 25% of the available material of any species was consumed within the time period (range 7.0 to 23.9%) (Table 1). Trials were conducted during major morning or evening feeding periods during 3 times of the year representing major growth phases of the woody plants. To minimize selection bias by deer, the same species was offered to each deer and only 1 species/day was used. Trial 1 was in June 1988 during stem elongation of the browse. Trial 2 was in August 1988

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Published with approval of the director, Texas Agr. Exp. Sta. as TA-27009.

Manuscript accepted 13 April 1991.

Table 1. Mean mass (g) and standard error (SE) of herbage on 20 branches/species of browse before and after offering to deer to determine instantaneous intake rate during 3 plant development stages on La Copita Research Area.

Species	New leaf development				Stem elongation				Full leaf development			
	Before	SE	After	SE	Before	SE	After	SE	Before	SE	After	SE
Spiny hackberry	(g)		(g)		(g)		(g)		(g)		(g)	
Spiny hackberry	27.4	2.3	23.5	2.2	38.7	2.9	32.9	2.7	34.7	2.1	29.4	1.9
Brasil	31.5	2.1	28.2	2.0	30.4	1.7	27.6	1.7	39.1	2.2	35.1	2.1
Guajillo	32.2	2.3	24.5	2.4	29.3	2.2	22.5	1.9	43.4	1.9	35.1	2.2
Texas persimmon	37.1	2.5	34.5	2.3	41.2	3.2	36.9	3.1	25.9	1.6	23.9	1.6
Lime pricklyash	30.2	1.9	25.5	1.7	29.8	1.9	23.7	1.9	35.9	1.9	29.3	1.8
Blackbrush	25.6	1.5	23.8	1.4	23.2	1.4	20.7	1.3	49.5	2.9	44.0	2.9
Coma	26.5	2.0	23.6	1.9	16.8	1.2	14.2	1.1	33.5	2.1	31.0	2.2
Huisache	27.6	1.3	24.2	1.3	9.5	0.6	7.7	0.6	20.9	1.5	15.1	1.3
Kidneywood	12.5	0.8	11.2	0.9	18.5	1.1	16.2	1.1	16.1	1.3	14.2	1.1

during full leaf development. Trial 3 was in May 1989 during new leaf development.

Plant Morphology

To evaluate how morphological characteristics correlated to IIR and INIR, 10 branches of each browse species were measured for thorn density (number/20-cm terminal segment), total weight of green leaves, and leaf weight/stem weight ratio. Mean leaf length was taken from Vines (1960).

Nutrient Concentration

Quality of woody plant foliage was estimated from hand-plucked samples of each species collected immediately after observing the feeding behavior of the deer during the intake trials. Care was taken to select only plant parts actually eaten by deer. Grab samples were dried for 48 hours at 50° C and then ground in a Wiley mill to pass a 1-mm screen. Diet quality analysis included percent crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent fiber nitrogen (ADFN) and was expressed on an organic matter (OM) basis. Crude protein was determined using standard micro-kjeldahl techniques (A.O.A.C. 1970). Neutral detergent fiber, ADF, and ADFN were determined by nonsequential procedures of Goering and Van Soest (1970). Estimates of INIR were derived by multiplying nutrient concentrations (g/100g OM) by the recorded intake rate (g/min).

Preference Indices

Preference indices were determined concurrently using 2 techniques by offering all 9 browse species to all deer simultaneously for 15 min. Branches similar in size to those used in the intake trials were stapled to 2 sawhorses (approximately 2-m long and 0.5-m high) so that the branches extended outward from both sides. Branches were of sufficient size so that no more than a mean of about 50% of available material of any species was consumed within the time period (range 2.6 to 51.4%) (Table 2).

Four branches (1 for each deer) of each browse species were arranged randomly along the board. For the first technique, branches were weighed immediately before and after offering to determine the amount of material of each species consumed. Weights of material removed, calculated as a percentage of available material by species, were ranked and the species with the highest percentage of material removed was considered the most preferred. For the second technique, a preference index was determined using the amount of time spent browsing each species by recording which species each deer was eating at 15-sec intervals. Percent time was ranked on a frequency basis and the species with the highest frequency was considered the most preferred.

Statistical Analysis

Data for IIR were analyzed by analysis of variance using the GLM procedure in SAS (SAS 1985). Instantaneous intake rate of browse species constituted the dependant variable, individual deer were used as replications, and species × deer was used as the error term because species and deer did not interact ($F = 1.27, 24, 8 \text{ df}, P = 0.23$). Following a significant F test, the protected Least Significant Difference (LSD) procedure (Steel and Torrie 1960) was used to identify differences in means. Pearson rank correlation was used to determine relationships of IIR and INIR rankings to ranks of plant morphological attributes, and to the ranks of the 2 preference indices to examine the comparability of techniques. Because our plants showed little seasonal variation in leaf mass, leaf weight/stem weight ratio, and thorn density, correlations to IIR and INIR are presented only for 1 trial.

Results and Discussion

Instantaneous Intake/Plant Morphology

Of the plant morphological attributes considered, mean leaf mass and leaf weight/stem weight ratio showed significant ($P < 0.05$) positive correlations ($r = 0.75$ and 0.65 , respectively) with IIR

Table 2. Mean mass (g) and standard error (SE) of herbage on 4 branches/species of browse before and after offering to deer to determine preference by amount of material consumed during 3 plant development stages in La Copita Research Area.

Species	New leaf development				Stem elongation				Full leaf development			
	Before	SE	After	SE	Before	SE	After	SE	Before	SE	After	SE
Spiny hackberry	(g)		(g)		(g)		(g)		(g)		(g)	
Spiny hackberry	61.5	5.8	57.0	5.2	49.3	7.5	30.4	6.7	77.4	11.4	53.2	5.1
Brasil	36.2	0.3	32.0	0.7	80.6	7.1	57.8	3.7	59.9	10.8	41.3	9.2
Guajillo	36.2	5.5	28.5	6.8	45.5	5.6	31.4	4.6	35.9	7.2	17.6	0.6
Texas persimmon	47.9	1.1	41.3	2.6	120.7	15.5	108.8	11.7	49.6	7.6	43.6	5.8
Lime pricklyash	47.6	3.6	45.0	3.8	46.6	8.8	32.2	7.5	43.4	4.2	21.1	2.4
Blackbrush	34.2	2.6	33.3	2.5	59.2	9.4	52.3	8.6	41.8	3.8	37.7	3.4
Coma	54.9	3.8	49.9	3.4	60.0	5.5	47.8	6.0	33.0	2.8	24.4	1.7
Huisache	26.9	2.1	25.1	1.7	32.0	5.0	27.1	4.2	29.5	6.4	23.6	5.6
Kidneywood	46.7	3.4	43.9	3.0	33.6	4.6	29.9	4.4	21.1	2.1	15.1	0.8

Table 3. Plant morphological attributes correlated with instantaneous intake rate (IIR) (g/min) of dry matter and instantaneous nutrient rate (INIR) (g nutrient/min) of crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent fiber nitrogen (ADFN) by white-tailed deer during Trial 1 on La Copita Research Area.

Species	Plant attributes			
	Leaf ¹ mass (g)	Leaf ² length (cm)	Thorn ¹ density (No./20 cm)	Leaf/stem ratio
Spiny hackberry	6.3	3.5	11.9	1.8
Brasil	6.0	2.3	16.5	1.0
Guajillo	4.8	12.7	0	2.1
Texas persimmon	4.6	4.0	0	0.4
Lime pricklyash	2.8	8.9	8.3	1.4
Blackbrush	2.7	1.7	36.4	0.7
Coma	2.3	2.5	7.3	0.5
Huisache	1.4	6.4	23.1	1.0
Kidneywood	1.1	4.5	0	0.3
Correlation coeff. (r)				
for IIR	0.75*	0.37	-0.39	0.65*
for INIR-CP	0.50	0.67*	-0.47	0.56
for INIR-NDF	0.73*	0.32	-0.27	0.59
for INIR-ADF	0.73*	0.22	-0.37	0.48
for INIR-ADFN	0.68*	0.53	-0.30	0.81*

¹Mean from terminal 20 cm of 10 randomly selected branches/species.

²Mean leaf length from Vines (1960).

*Correlation coefficient significantly ($P<0.05$) different from zero.

(Table 3). Mean leaf length and thorn density were uncorrelated. Species with growth forms that provided larger quantities of lush leaves at stem ends and with few or small stems were readily consumed. In free ranging goats, Hanley (1982) found the amount and accessibility of palatable forage influenced the degree of selectivity. Apparently the relatively small mouth size of deer and goats (Hanley 1982) is counter adapted to many plant defenses and allows for harvest of palatable plant parts despite presence of spines or thorns. This agrees in part with Hervey (1989), who found mean leaf size and leaf crown volume weight (g/m^3) were highly correlated with IIR of deer and goats while spinescence and amount of volatile oils were poorly correlated. Likewise, Cooper and Owen-Smith (1986) observed that plant prickles, unless coupled with small leaf size, were ineffective in deterring browsing ungulates in Africa. Wickstrom et al. (1984) also found that dry matter intake by mule deer (*O. hemionus hemionus*) was relatively insensitive to standing crop biomass.

Leaf mass also showed significant ($P<0.05$) positive correlations with INIR of NDF ($r=0.73$), ADF ($r=0.73$), and ADFN ($r=0.68$) (Table 3). Leaf length showed a significant ($P<0.05$) correlation ($r=0.67$) with INIR of CP. While not significant ($P>0.05$), thorn density tended to be negatively correlated to IIR and INIR.

Guajillo consistently ranked highest in IIR during all trials (Fig. 1). Although leaf length was poorly correlated to IIR (Table 3), guajillo's relatively long leaves, high leaf weight/stem weight ratio, and growth form where leaves and small twigs tend to be clustered on the terminal end of single large stems, likely presented the animals with large, leafy bites free from obstructions. Hervey (1989) found deer harvested guajillo almost 3.5 times greater than any other browse species tested. Lime pricklyash and spiny hackberry also were consistently prominent in IIR (Fig. 1). Although armed, both of these species exhibited a relatively high leaf weight/stem weight ratio (Table 3) allowing for a high intake rate. Texas persimmon ranked high during the stem elongation phase but dropped to a low level for the other 2 periods (Fig. 1). Hervey (1989) also found Texas persimmon to have a high IIR during June. Although persimmon had a high leaf mass, relatively large leaves, and no spinescence, the low leaf weight/stem weight ratio (Table 3) indicated animals would have to contend with numerous

stems while browsing. Vines (1960) described the growth form of Texas persimmon as intricately branched. Possibly during the stem elongation phase, terminal branches were pliable and did not hinder browsing as extensively. Brasil and blackbrush had a high IIR only during the full leaf development stage (Fig. 1). Both of these species are highly armed and have relatively small leaves (Table 3). Full mature leaves may be necessary to allow efficient harvest. To illustrate this, mean intake rate of all 9 species was estimated at 7.0 g/min during new leaf development, 7.8 g/min

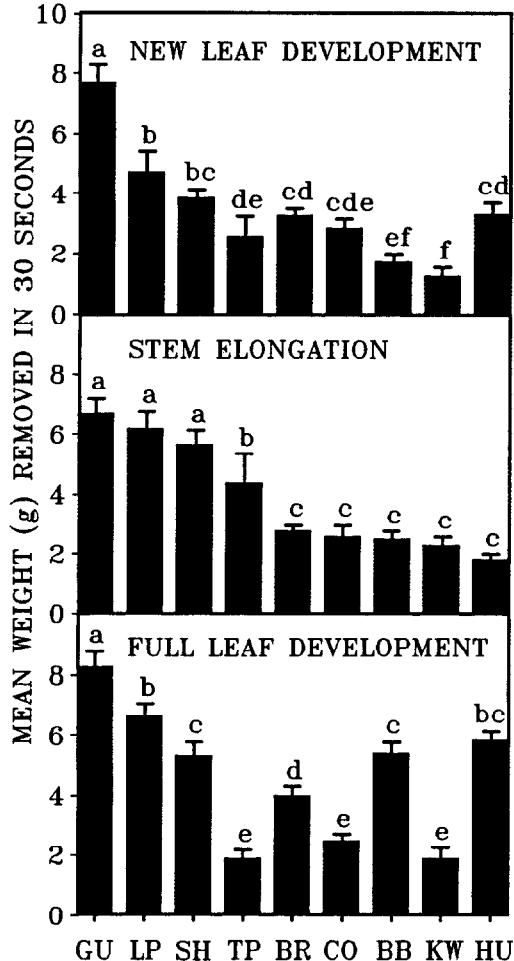


Fig. 1. Instantaneous intake rate (IIR) by white-tailed deer of 9 browse species during 3 plant development stages (mean and standard error). Different letters above bars indicate significant differences ($P<0.05$) within a growth stage according to protected Least Significant Difference. GU = guajillo, LP = lime pricklyash, SH = spiny hackberry, TP = Texas persimmon, BR = brasil, CO = coma, BB = blackbrush, KW = kidneywood, and HU = huisache.

during stem elongation, and 9.2 g/min when all species had attained mature status. Huisache, another prominently armed species with a low leaf weight/stem weight ratio, showed a high IIR during the full leaf stage but also was ingested relatively efficiently during new leaf development (Fig. 1). Instantaneous intake rate for coma and kidneywood was low for all trials.

Instantaneous Intake/Nutrient Concentration

Crude protein of the browse plants declined as the plants matured (Table 4). Verme and Ullrey (1974) estimated that dietary CP levels of 13–20% are sufficient for growth and reproduction in white-tailed deer. All browse species maintained or exceeded required CP during the 3 growth stages, similar to findings of Everitt and Gonzalez (1981) and Meyer and Brown (1985).

Table 4. Crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent fiber nitrogen (ADFN) of 9 browse species used to determine instantaneous intake rate (IIR) (g/min) of white-tailed deer during 3 plant development stages (% organic matter basis).

Species	New leaf development				Stem elongation				Full leaf development			
	CP	NDF	ADF	ADFN	CP	NDF	ADF	ADFN	CP	NDF	ADF	ADFN
Spiny hackberry	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Brasil	32.3	37.4	21.1	6.8	27.7	42.7	25.2	4.0	24.1	35.2	20.6	3.6
Guajillo	20.1	44.5	27.4	3.3	16.3	43.2	23.9	3.8	13.8	38.2	24.1	4.2
Texas persimmon	21.2	62.0	37.9	2.9	18.7	52.4	29.5	4.2	15.6	49.3	26.9	3.4
Lime pricklyash	15.4	53.8	39.3	1.1	12.8	47.7	35.2	1.6	13.8	43.4	33.6	1.9
Blackbrush	24.8	31.9	19.5	5.0	18.9	27.2	19.9	3.3	18.5	33.5	23.4	2.4
Coma	17.0	64.2	57.6	2.7	13.3	56.6	43.1	2.5	15.8	55.6	43.4	3.1
Huisache	14.6	35.1	26.0	3.2	13.4	30.4	23.7	2.8	12.3	30.9	25.8	2.6
Kidneywood	27.8	54.6	28.9	6.3	26.2	55.9	31.3	3.6	20.7	46.8	25.5	5.0
Correlation coeff. for IIR	24.1	43.1	24.7	3.6	22.1	45.4	26.3	3.2	15.5	52.5	31.7	2.6
	0.48	-0.15	0.30	0.38	-0.05	-0.40	-0.33	0.42	0.56	-0.05	-0.30	0.33

Trends in NDF and ADF during the various growth stages were not distinct (Table 4). Several species unexpectedly exhibited a higher fiber content during new leaf development than during the more mature stages. This may be partially explained by far below normal precipitation (approximately 97% below long term monthly median) and above normal temperature during May 1989 (Table 5). Low moisture and high temperature may interact to increase

preference indices based on weight of forage removed and amount of time spent browsing (Table 6). A significant ($P<0.05$) positive

Table 6. Pearson correlations of instantaneous intake rate (IIR) (g/min) and instantaneous nutrient intake rate (INIR) (g nutrient/min) during 3 plant development stages and preference indices based on weight (WT) of forage removed and time (TIME) spent browsing by white-tailed deer. Nutrients investigated included crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent fiber nitrogen (ADFN).

Comparison	New leaf development	Stem elongation	Full leaf development
IIR with WT	0.48	0.71*	0.20
IIR with TIME	0.48	0.39	0.23
INIR-CP with WT	0.47	0.35	0.45
INIR-CP with TIME	0.48	-0.05	0.47
INIR-NDF with WT	0.38	0.53	-0.05
INIR-NDF with TIME	0.32	0.22	0.15
INIF-ADF with WT	0.38	0.60	0.07
INIR-ADF with TIME	0.32	0.33	0.15
INIR-ADFN with WT	0.50	0.70*	0.22
INIR-ADFN with TIME	0.52	0.36	0.33
WT with TIME	0.73*	0.87*	0.70*

*Correlation coefficient significantly ($P<0.05$) different from zero.

correlation ($r = 0.71$) was found between IIR and weight of forage removed only during the stem elongation stage. Positive correlations between weight removed and time spent browsing, however, were significant ($P<0.05$) during all 3 plant growth stages ($r = 0.73$ for new leaf development $r = 0.87$ for stem elongation, and $r = 0.70$ for full leaf development), indicating the 2 techniques closely agreed in species rankings.

A number of factors may affect preference and all relative preference indices have shortcomings (Krueger 1972, Cock 1978, Johnson 1980, Loehle and Rittenhouse 1982, Owen-Smith and Cooper 1987). A fundamental shortcoming of comparing usage and availability data to determine preference is the often arbitrary decision about the array of components actually available to an animal (Johnson 1980). Inclusion or exclusion of availability components can affect results. In determining preference indices in our study, availability components were set equal to each other within all trials. Our primary purpose was to rank the various species from most to least preferred under a specified condition. Use of rank data avoids absolute statements about preference or avoidance (Johnson 1980).

When presented with all browse species simultaneously, deer did not appear to select forages based solely on leaf size, spinescence, or possible rate of intake. Guajillo, for example, ranked first in IIR for all trials but ranked second to fourth in weight of forage

Table 5. Thirty year temperature (C) means and median precipitation (mm) from Alice, Texas and means for study period on La Copita Research Area.

	Thirty year mean			May 1989	June 1988	Aug 1988
	May	June	Aug			
High temperature (° C)	31.5	34.3	36.1	35.3	34.4	36.6
Low temperature (° C)	19.9	22.4	23.0	22.6	21.7	23.5
Precipitation (mm)	73.4	71.6	34.0	2.5	53.8	28.7

cell wall components through increased lignification and more rapid conversion of photosynthetic products to structural components despite plant age (Van Soest 1982). June and August 1988 had precipitation 25% and 16% below long-term monthly median, respectively, with average temperatures (Table 5). Meyer and Brown (1985) found lower NDF concentrations in some winter forages compared to autumn samples following rains that broke a summer-long drought. Nutrient and fiber concentrations in our study were not significantly ($P>0.05$) correlated to IIR during any plant development stage (Table 4).

Acacia species (guajillo, huisache, and blackbrush) and Texas persimmon tended to possess the highest fiber concentrations throughout the growing season (Table 4). Even though deer ingested guajillo faster than the other browse species, the high fiber content would likely require more microbial cellulose digestion and longer retention time in the rumen. Schoonveld et al. (1974) felt the small rumen-reticula, omasa, and abomasum size of mule deer would prevent fibrous material from remaining in the rumen long enough for adequate digestion of lignified fiber. Fiber concentrations in lime pricklyash and spiny hackberry tended to be the lowest of all species tested indicating a relatively high availability of cell solubles. Low fiber, high IIR, and high CP content may make lime pricklyash and spiny hackberry the most profitable plants of the species studied for nutrient intake by deer. Meyer et al. (1984) also found spiny hackberry and lime pricklyash were high quality summer forages for deer.

Instantaneous Intake/Preference Indices

Instantaneous intake rate and INIR were poorly correlated with

removed and fourth to seventh in time spent browsing (rank data not shown). Brasil, coma, spiny hackberry, and lime pricklypear consistently ranked first or second in weight removed or time spent browsing. Although brasil and coma had relatively low IIR, deer appeared to select for these species based on palatability factors not measured. Cooper and Owen-Smith (1986) found that intake rate was unrelated to acceptability of browse species for goats and impalas (*Aepyceros melampus*). For larger animals such as kudu (*Tragelaphus strepsiceros*), an intake rate of <2 g/min negatively influenced acceptance. Instantaneous intake rates among species in our study ranged from an estimated 2.6 to 16.6 g/min (Fig. 1). Therefore, we assume the deer in our study were selecting forages based on factors other than potential intake rate.

Given a limited number of choices (9 species in our case) with little spatial variation, a purely generalist foraging strategy (Nudds 1980) would suggest the deer should respond by feeding randomly among the species offered. However, when deer were exposed to all browse species at once, feeding was not sequential from branch to branch. Rather, each animal appeared to avoid some species while accepting others. This is supported by our preference ranks showing some species were consumed more and maintained longer feeding durations than others. However, the deer did consume parts of all species presented. While not designed to examine foraging theory in detail, our results appear to support the concept that white-tailed deer are selective feeders and attempt to obtain a nutrient-optimizing diet within a fixed bulk of food (Nudds 1980).

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Utilization of larkspur by sheep

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Abstract

Sheep are more resistant to larkspur (*Delphinium* spp.) poisoning than are cattle, and may be used as a biological tool to graze larkspur prior to cattle turn-in to reduce the risk of cattle poisoning. Sheep utilization of 3 species of larkspur was measured at 3 phenological growth stages (vegetative, bud, and flower) at 5 locations. Utilization of waxy larkspur (*D. glaucescens* Wats), varied among years at Ruby, Mont. Use of duncecap larkspur (*D. occidentale* S. Wats) at Oakley, Ida., was uniformly higher in all 3 growth stages due to closed herding practices. Use of tall larkspur (*D. barbeyi* Huth) increased as it matured. Trailing sheep through larkspur patches, or bedding them in patches greatly increased trampling of larkspur stalks and utilization of heads and leaves.

Key Words: *Delphinium* spp., poisonous plant, sheep grazing, biological tool

Poisoning from ingestion of larkspur (*Delphinium* spp.) is the leading cause of cattle deaths on mountain rangeland (Aldous 1917, Nielsen and Ralphs 1988). Sheep, on the other hand, are more resistant to larkspur poisoning than cattle (Marsh et al. 1934, Olsen 1978), thus, forward grazing by sheep may be an effective strategy for reducing the availability and/or acceptability of larkspur to grazing cattle. This in turn should reduce cattle losses from larkspur poisoning.

Previous research examining the impact of forward grazing by sheep varied as a function of species of larkspur and season. For example, Marsh et al. (1934) reported sheep grazing stands of low larkspur (*Delphinium nelsonii* Greene) reduced incidence of cattle losses. Aldous (1917) reported that sheep grazing immature duncecap larkspur (*D. occidentale* S. Wats) early in the growing season eliminated subsequent poisoning of cattle. However, sheep grazed other forage in preference to tall larkspur (*D. barbeyi* Huth), thus increasing the threat to cattle.

The underlying hypothesis of this study is that forward grazing by sheep will subsequently reduce cattle losses to larkspur poisoning by reducing availability and/or acceptability of larkspur. This can be accomplished by sheep ingesting and/or trampling larkspur during the early portion of the growing season. The broad objective of the studies reported herein was to examine the impact of sheep grazing on 3 species of larkspur during early growth stages. Study 1 examined the variation in consumption of waxy larkspur (*D. glaucescens* Wats) in the bud growth stage over a 4-year period. Study 2 was designed to quantify the amount of duncecap and tall larkspur grazed and/or trampled by sheep during the vegetative, bud, and flower growth stages among 4 locations during a single year. In addition, the relative impacts of trampling and defoliation were examined when sheep were in the grazing, trailing, or bedding modes at 2 of these locations. Alkaloid concentrations in larkspur species were measured at each site to determine if alkaloid level influenced utilization of larkspur.

Methods

Study 1

The study was conducted in the upper Ruby River Valley 93 km

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Manuscript accepted 15 April 1991.

south of Sheridan, Mont. The Upper Ruby Cattle Association traditionally graze 2,700 cows and yearlings on the allotment from June to October. Larkspur poisoning occurs intermittently in 3 higher elevation pastures, with the most recent event (1981) resulting in the deaths of 50 cattle. This prompted a change in management to include grazing a flock of sheep in these pastures 2 to 4 weeks prior to cattle turn-in.¹

The study site was at 2,600 m elevation on a gentle sloping, north exposure ridge. Habitat type was mountain big sagebrush [*Artemesia tridentata* var. *vaseyana* (Rydb.) J. Boivin]/Idaho fescue (*Festuca idahoensis* Elmer). Waxy larkspur density averaged 4.0 plants/m².

Four, 30-m permanent transects were established and 25 waxy larkspur plants per transect were permanently marked for study prior to sheep grazing. A band of 1,000 yearling ewes grazed the study area from 1987–1989 spending 1.5 hours grazing on 25–26 June 1987, and 4 hours on 22–23 June 1988. On 27 June 1989, they grazed over the site for about 1 hour before bedding on 2 of the transects for about 4 hours during mid-day. The band then drifted through the 2 other transects as they exited the area. In 1990, a band of 650 ewes with lambs stayed 16 days in the general area grazing intermittently on a 20 ha patch of waxy larkspur within which our study site was located.

Following grazing, total number of stalks per marked plant, number of flowering racemes (heads) decapitated, and defoliation of leaves were recorded in all 4 years.

Study 2

Utilization of duncecap and tall larkspur was measured at 4 locations in 1989 at the vegetative, bud, and flower growth stages to compare the amount of larkspur consumed or trampled among growth stages. Larkspur patches were selected in grazing allotments where sheep would normally graze at the specified growth stages. Since the objective of this study was to measure utilization under normal grazing conditions, time spent in larkspur stands, grazing pressure, and utilization of associated species varied between sites and locations. Table 1 gives details of the location, habitat type, time sheep grazed the areas, and sampling design.

Oakley, Idaho

Utilization of duncecap larkspur was measured on the South Hills, 24 km west of Oakley, between 2,200 and 2,400 m elevation. Utilization during the vegetative stage was measured at Worm Corral. Habitat type was snowberry (*Symphoricarpos oreophilus* Gray)/slender wheatgrass (*Elymus trachylcaulus* (Link) Gould ex Shinners). A band of 1,900 ewes with lambs were herded onto the patch for the entire day of 8 June. Three areas were delineated where sheep: (1) grazed through in an open herd (grazing mode); (2) bedded during the middle part of the day (bed mode); and (3) trailed out in a tight herd (trailing mode).

Utilization during the bud stage was measured at Willow Creek where larkspur occurred in the bottoms of draws in the mountain big sagebrush/basin wildrye (*Elymus cincereus* Scribn. & Merr.) habitat type. Utilization during the flower stage was measured at Gravel Springs in an aspen (*Populus tremuloides* Michx)/snowberry habitat type.

¹Alexander, J.D. III and J.E. Taylor 1986. Sheep utilization as a control method on tall larkspur infested cattle range. Abstract 241. 39th Annual Meeting, Society for Range Management, Kissimmee, Fla. Feb. 9–14, 1986.

Table 1. Sampling scheme used to estimate sheep utilization of 3 species of larkspur.

Larkspur	Location	Elev- ation	growth stage	Sampling data	Habitat type	Larkspur plant density	Activity mode	Number of larkspur patches	Number of transects per patch ¹	Average stems per plant	Average patch size	Time spent in area	Flock size
No./m ²													
Waxy	Ruby, MT	2600m	Bud		Mountain big sagebrush/ Idaho fescue	4	Graze	1	10	3	20	1-14	
Duncecap	Oakley, ID	2200m	Vegeta- tive	8 June 1989	Snow- berry/ slender wheatgrass	7.5	Graze Trail Bed	1 1 1	5 4 5	13 13 13	4 2 2	1	1900 ewes with lambs
		2400m	Bud	14 July	Mountain big sagebrush/ basin wildrye		Graze	3	5	11	3	14	
		2500m	Flower	10 Aug.	Aspen/ snowberry		Graze	2	5	7	6	3	
Barbeyi	Ferron, UT	3200m	Vegeta- tive	1 July 1989	Larkspur/ western coneflower	2.4	Graze Trail	2 2	5 5	31 31	3 2	3	2000 ewes with lambs
		3000m	Bud	20 July	Aspen/tall forb		Graze	2	5	12	2	10	
		3200m	Flower	15 Aug.	Larkspur/ western coneflower		Graze	4	5	28	5	7	
	Salina, UT	3000m	Bud	18 July 1989	Aspen/ larkspur/ mountain brome	2.2	Graze	3	5	7	5	20	2000 ewes with lambs
	Cedar, UT	3000m	Flower	1 Aug.			Graze	2	5	14	2	12	
			Bud	19 July 1989	Aspen/ orchard grass	3.0	Graze	1	10 ²	3	12	43	200 ewes

¹Ten larkspur plants were selected on each paced transect at 5 or 10 step intervals.²Ten permanent transects were established at Cedar and 10 plants were marked by a stake on each transect.

Ferron, Utah

Utilization in both the grazing and trailing activity mode was measured during the vegetative growth stage of tall larkspur at Ferron Reservoir, 46 km west of Ferron. The habitat type was a larkspur/western coneflower (*Rudbeckia occidentalis* Nutt) type interspersed among Engelmann spruce (*Picea pungens* Engelm.) at 3,200 m elevation. This band was managed as an open herd and were not gathered to bed grounds, thus precluding utilization in the bed mode.

Utilization during the bud stage was measured in an aspen/tall forb habitat type at 3,000 m elevation. Utilization during the flower stage was also measured in the larkspur/western coneflower habitat type about 2 km from the area grazed in the vegetative stage.

Salina, Utah

The study area was located 40 km east of Salina at an elevation of 3,000 m. Sheep did not enter the allotment until tall larkspur was in the bud growth stage, thus utilization was measured for only the bud and flower stages. Habitat type was aspen/larkspur/mountain brome (*Bromus carinatus* H & H).

Cedar City, Utah

Utilization of tall larkspur on Cedar Mountain, 35 km east of

Cedar City, was measured in the early grazed pasture of a deferred rotation grazing system. Habitat type was aspen/orchard grass (*Dactylis glomerata* L.) at 2,800 m elevation. No utilization was observed on these plants during the vegetative stage, but all plants were heavily grazed during the bud stage, thus utilization was measured only during the bud stage.

One to 4 larkspur patches were selected for each growth stage at each location (Table 1). Five paced transects were established in each patch and 10 plants per transect were selected using step point procedures. Measurements taken were: number of stalks per plant, number of stalks trampled, number of reproductive heads grazed, number of grazed and ungrazed leaves, and overall number of plants grazed.

Alkaloid concentration was measured in larkspur plant parts (leaves and reproductive raceme) at each location at the time of grazing. Samples were air dried and analyzed for total alkaloid concentration (Manners and Ralphs 1989). Percentage utilization of larkspur leaves and heads were correlated with total alkaloid concentration in the respective larkspur plant parts and correlation coefficients (*r*) were calculated to determine if larkspur utilization was related to alkaloid levels in the plant.

Data Summarization and Analysis

Larkspur utilization at all locations and growth stages was estimated by counting number of heads decapitated and leaves grazed on each sampled plant. Number of broken stems was counted to access impact of trampling. The total number of plants grazed per transect was determined and percentage calculated. Since the number of stalks per plant differed greatly between species and locations (Table 1), we summed total number of stalks and leaves present by transect and then calculated percentage of heads and leaves grazed, and stems trampled. Percentage data were transformed by arcsin and analyzed by analysis of variance (ANOVA), rather than by Chi Square because Chi Square analysis of count data would have precluded evaluating variability among transects or patches.

Transects were used to test for differences in utilization of waxy larkspur between years in study 1. In study 2, utilization was not measured at all growth stages at each location because of changes in grazing and herding patterns. Thus, data were analyzed separately for each location. Data were analyzed in a nested model in which transects were nested within patches and used to test for difference in utilization between growth stages. Utilization and trampling during different activity modes (grazing, trailing, and bedding modes at Oakley and grazing and trailing modes at Ferron) were compared in a similar model. Means were separated by Duncan's multiple range test. Nontransformed means are presented in the tables.

Results and Discussion

Study 1

Sheep consumed varying amounts of waxy larkspur over the years at Ruby. Percent of heads grazed on marked plants declined from 70% in 1987, to 14% in 1989, but increased to 73% in 1990 (Table 2). Stem height was reduced an average of 36% when the

Table 2. Sheep utilization (%) of waxy larkspur plants during bud stage on permanent and paced transects at Ruby River, Montana.

Transect type	Year	Heads grazed	Stalks having leaves grazed
%			
Permanent	1987	70 ^a	0 ^c
	1988	36 ^b	22 ^b
	1989	14 ^c	25 ^b
	1990	73 ^a	89 ^a

^{abc}Means in the same column transect type not followed by the same letter are significantly different ($P < .05$).

heads were grazed. Sheep consumed no larkspur leaves in 1987, but use of leaves increased to 89% in 1990.

There was no apparent relationship between amount of time sheep spent on a site and degree of larkspur use. In the first year of the study, sheep spent only 1.5 hours on the site and selectively removed 70% of the heads. They selectively grazed most of the elongating buds, with little apparent use of associated plant species. This was as desired because larkspur heads are very toxic and preferred by cattle. In 1990, sheep spent 14 days in the area and repeatedly grazed over the transects, heavily utilizing both larkspur heads and leaves. Larkspur utilization was low in the 2 middle years.

In 1989, there was a difference in utilization among transects. Sheep bedded on 2 of the transects and trampled 37% of the marked plants, grazed 28% of the reproductive heads, and 48% of the plants had leaves grazed. Very little larkspur was grazed in the grazing mode on the other 2 transects.

The sheep owner observed over the years that sheep preferred

the elongating larkspur bud (Joe Helle, personal communication, 1988). He stated that sheep made little use of waxy larkspur in the years they grazed the allotment prior to the bud stage. We observed that sheep rejected waxy larkspur in the flowering stage. Comments from the herder indicate that sheep prefer the waxy larkspur bud when it is crisp and moist, when it is covered with dew in the early morning, or following storms. Bedding on waxy larkspur patches (as in 1989) and grazing over the patches several times (as in 1990) appear to increase utilization and trampling.

Study 2

Oakley

Sheep grazed almost all of duncecap larkspur plants during all 3 growth stages (Table 3). There were slight differences in the percent

Table 3. Utilization (%) by grazing sheep of 2 species of larkspur in 4 grazing allotments during 3 growth stages.

Larkspur species	Location	Growth stage	Plants grazed	Stems trampled	Heads grazed	Leaves grazed
%						
Duncecap	Oakley	Veg	98 ^a	27 ^a	55 ^b	29 ^a
		Bud	92 ^{ab}	36 ^a	79 ^a	21 ^a
		Flower	85 ^b	30 ^a	56 ^b	31 ^a
Tall	Ferron	Veg	5 ^b	16 ^a	0 ^c	0 ^c
		Bud	93 ^a	20 ^a	19 ^b	45 ^a
		Flower	91 ^a	23 ^a	29 ^a	25 ^b
	Salina	Bud	22 ^b	12 ^b	5 ^b	1 ^b
		Flower	90 ^a	21 ^a	50 ^a	48 ^a
	Cedar City	Veg	0	0	0	0
		Bud	100	45	50	91

^{abc}Means within the same column within locations not followed by the same letter are significantly different ($P < .05$).

of reproductive heads grazed between growth stages (55–79%) but not in percentage of leaves grazed (21–29%). An average of 31% of the stems were trampled. The relatively high level of larkspur utilization in all growth stages differs from trends of use in other locations. Sheep at Oakley stayed in a fairly tight bunch, due to being tormented by gnats and closed herding practices. Nonselective grazing while in a tight group, may account for the high larkspur utilization.

Ferron

Very little tall larkspur was utilized in the vegetative stage (Table 3). The extremely high concentration of alkaloids in the vegetative leaves (6.75%, Table 5) may have contributed to their avoidance. Ralphs et al. (1988) hypothesized that there is a negative relationship between alkaloid levels and palatability of larkspur.

Sheep increased consumption of both heads and leaves of tall larkspur as plants matured from the vegetative to bud stage. The number of plants grazed increased from only 5% in the vegetative stage to 91–93% in the flower and bud stage (Table 3).

Sheep consumed slightly more of the larkspur heads in the flowering stage compared to the bud stage. However, substantially more leaves were consumed in the bud stage (Table 3). Tall larkspur patches sampled during the bud stage were near a small watering pond. Sheep likely passed through these patches each day grazing to and from water, and thus had more opportunity to graze larkspur. The larkspur patches sampled during the flower stage were more than 1 km from water and sheep had to travel a greater distance to reach the larkspur patches.

Salina

Sheep were not on this allotment when larkspur was in the vegetative growth stage. Only 22% of tall larkspur plants were grazed in the bud stage compared to 90% in the flower stage (Table

Table 4. Differential use of larkspur during grazing, trailing and bedding modes at Ferron and Oakley during the vegetative growth stage.

Larkspur species	Location	Activity	Plants grazed	Stems trampled	Heads grazed	Leaves grazed
%						
Duncecap	Oakley	Graze	98 ^a	27 ^b	55 ^b	29 ^b
		Trail	85 ^b	87 ^a	48 ^b	11 ^b
		Bed	100 ^a	90 ^a	68 ^a	83 ^a
Tall	Ferron	Graze	5 ^a	16 ^b	0 ^a	0 ^a
		Trail	4 ^a	48 ^a	0 ^a	0 ^a

^{abc}Means within the same column within locations followed by the same letter are not significantly different ($P < .05$), as determined by Duncan's multiple range test.

3). Fifty percent of the reproductive heads and 48% of the leaves were grazed during the flower stage. The larkspur patch near water sustained heavier use compared to one 1.6 km away due to its more frequent visitation by sheep.

Cedar City

Sheep did not graze tall larkspur in the vegetative stage. However, they consumed or trampled almost all of the larkspur plants during the bud stage. Over 90% of the leaves and 50% of the heads were grazed, and 45% of the stems were trampled (Table 3).

The heavy use of tall larkspur in the bud stage at this site can be attributed to several factors. Unlike the other locations where the sheep were periodically moved to fresh feed, this pasture was the heavily grazed pasture of a deferred rotation grazing system. Grazing pressure increased as other forage was depleted. Utilization of orchard grass and Kentucky bluegrass (*Poa pratensis L.*) was 70% (Bowns, unpublished data). Utilization on other desirable forbs was not measured, but it was obviously greater than the utilization of these 2 key grasses. The sheep may have been forced to consume larkspur as other forage became limited. Two other reasons may account for larkspur's increased acceptability. Sheep generally graze larkspur later in the grazing season when summer rains wash aspen sap off its leaves (Bowns, personal observation). Larkspur may also have increased in palatability as it matured and alkaloid levels declined (Pfister et al. 1988a,b).

Activity Modes

Sheep trampled a larger number of larkspur stems during the trailing and bedding mode at Oakley and trailing mode at Ferron than they did in the grazing mode (Table 4). Furthermore, 80% of the trampled stems at Oakley were dry and desiccated after 30 days, while untrampled stems were green and growing. Sheep also consumed more duncecap larkspur heads and leaves (68% of heads and 83% of leaves) while they were milling about in the bedding mode at Oakley. No leaves were consumed in the trailing mode at Ferron, presumably due to the high alkaloid levels (Table 5).

Alkaloids

Alkaloid levels generally declined as the plants matured, except for tall larkspur heads at Ferron (Table 5). There was low correlation ($r = -.30$) between alkaloid level and larkspur consumption when both larkspur heads and leaves were included in the equation. When consumption of larkspur leaves and heads were analyzed separately, correlation between alkaloid level and consumption of larkspur leaves improved somewhat ($r = -.44$), while the correlation with heads declined ($r = -.05$). Ralphs et al. (1988) hypothesized that high levels of alkaloids in larkspur plant parts in early growth stages deterred grazing, and suggested a negative relationship between alkaloid levels and palatability. Cattle consumption of tall larkspur increased dramatically as plants matured beyond the flower growth stage (Pfister et al. 1988a,b). Sheep have also been observed to utilize both duncecap and tall larkspur leaves

Table 5. Total alkaloid concentration (%) in 3 species of larkspur, at 5 locations, during the vegetative, bud and flower growth stages.

Larkspur species	Location	Growth stage	Total alkaloids	
			Head	Leaf
Waxy	Ruby	1987 Bud	1.26	0.90
		1988 Bud	2.10	0.60
		1989 Bud	1.36	0.41
Duncecap	Oakley	Veg	—	2.60
		Bud	2.20	2.40
		Flower	1.74	.91
Tall	Ferron	Veg	—	6.75
		Bud	.91	1.45
		Flower	2.10	1.13
Salina	—	Bud	1.46	1.26
		Flower	.75	.78
Cedar	—	Bud	1.22	1.08

heavily during the later part of the growing season (authors' personal observations). Further research is necessary to determine the relationship between alkaloid levels and palatability.

Management Implications

Under some conditions, sheep will utilize large amounts of all 3 larkspur species. They may not voluntarily graze larkspur during the vegetative and bud stages of growth, but they may be compelled to utilize it by trailing or bedding on larkspur patches. Trailing sheep through larkspur patches increased the number of larkspur stalks trampled. The hollow stems break easily when trampled and are likely to senesce rapidly. Bedding sheep in larkspur patches increased both the number of stalks trampled and greatly increased utilization of larkspur heads and leaves. Intensive management of a sheep herd either by bedding or holding them on a larkspur patch may cause heavy non-selective grazing of larkspur. Further research is necessary to determine what level of larkspur use is required to reduce the risk of poisoning in cattle grazing afterward.

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Wyoming big sagebrush control with metsulfuron and 2,4-D in northern New Mexico

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Abstract

Field experiments conducted between 1982 to 1988 compared 2,4-D [(2,4-dichlorophenoxy)acetic acid] and metsulfuron [2-[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl) amino]carbonyl]amino]sulfonyl]benzoic acid] for control of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young) in northern New Mexico. Precipitation was near or above normal during years of herbicide applications. Broadcast sprays of 2,4-D at 2.2 kg/ha were most efficacious during rapid shoot elongation, but mortality averaged less than 38% from treatments applied over 4 separate years. Wyoming big sagebrush shoot growth was greatest in April and May compared to other months, but growth was highly variable among shrubs and probably reduced effectiveness of 2,4-D sprays. The optimum application timing for metsulfuron was during the late-flower growth and fruiting stages. Fall-applied metsulfuron at 0.035 kg/ha provided 65% Wyoming big sagebrush mortality compared to 27% when spring-applied. When metsulfuron was fall-applied at 0.07 kg/ha or higher, control averaged 88% following 3 annual applications. Combining metsulfuron at .0175 kg/ha plus 2,4-D at 1.1 kg/ha was comparable to or more effective than either herbicide applied alone in spring or fall. Total standing crop of grasses increased by nearly 300% after 1 or 2 growing seasons when Wyoming big sagebrush canopy cover was reduced by at least 75% following herbicide treatments.

Key Words: *Artemisia tridentata* ssp. *wyomingensis*, herbicides, herbage production, rangeland brush control

Herbicultural control of big sagebrush (*Artemisia tridentata* Nutt.) has been a common practice since the early 1950's in the intermountain region, and on the high plains of Wyoming, Montana, and the Dakotas (Evans et al. 1979). However, this practice has not been widely employed in the Colorado Plateau region (McDaniel and Balliette 1986). Control of big sagebrush with phenoxy herbicides, especially 2,4-D at 2.2 kg ae/ha, has been widely reported (Elwell and Cox 1950, Hormay et al. 1962, Hull and Vaughn 1951, Hyder and Snea 1962, Evans et al. 1979, Valentine 1980). Research and commercial experience has shown big sagebrush is easily controlled when phenoxy herbicides are applied in late spring-early summer during the period of active leaf and leader growth (Cornelius and Graham 1958; Hyder and Snea 1956, 1962; Hyder et al. 1962). Percent control usually decreases when big sagebrush is sprayed in summer (Sosebee 1983); however, Evans and Young (1977) reported 2,4-D to be equally effective in the intermountain region when applied in fall compared to spring.

According to Hyder (1954), big sagebrush mortality is enhanced by applying phenoxy herbicides at determined growth stages and when soil moisture is not limiting. Hormay et al. (1962) reported poor herbicide control on big sagebrush growing on dry sites, but

greater than 90% control when plants grew on relatively wet sites. Precipitation in northern New Mexico averages less than 6.5 cm from January to June, and this limits big sagebrush shoot growth (McDaniel and Balliette 1986). Application of phenoxy-like herbicides in this region, including 2,4-D, dicamba (3,6-dichloro-2-methoxybenzoic acid), triclopyr [(3,5,6-trichloro-2-pyridynyl)oxy]acetic acid) and clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) applied as sprays during May, June, or July have been largely ineffective, except at high use rates (Duncan and McDaniel 1988, Whisenant 1987). Most big sagebrush chemically controlled in northern New Mexico is treated with tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea). Tebuthiuron, which is applied to the soil and transported through the roots, can be applied irrespective of the growth stage of big sagebrush, killing about 90% of the shrubs at rates of 0.6 kg ai/ha or higher (McDaniel and Balliette 1986).

Recent research has been directed towards use of metsulfuron (2-[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]amino]sulfonyl]benzoic acid) for control of various rangeland weeds including multiflora rose (*Rosa multiflora* Wendl.) (Derr 1989), spotted knapweed (*Centaurea maculosa* Lam.) (Lass and Callahan 1989), Canada thistle (*Cirsium arvense* [L.] Scop.) (McKone 1989), and broom snakeweed (*Gutierrezia sarothrae* [Pursh.] Britt. and Rusby) (McDaniel and Duncan 1987). Metsulfuron is a member of the sulfonylurea group, which are potent inhibitors of plant growth at low application rates. Unlike 2,4-D, which induces a massive cellular proliferation of photosynthates in the meristematic tissue of plants (Anderson 1983), metsulfuron inhibits enzymes needed to produce essential amino acids valine and isoleucine. Under ideal conditions, metsulfuron applications result in rapid cessation of cellular growth and eventual plant death (Beyer et al. 1988). Because the mode of action of metsulfuron is different from that of 2,4-D, many growth and environmental conditions prescribed when spraying 2,4-D for big sagebrush control may not be applicable for metsulfuron treatments. The primary object of this study was to compare the effectiveness of metsulfuron and 2,4-D, applied at various rates, for control of Wyoming big sagebrush in northern New Mexico. Changes in herbaceous vegetation after treatments were also determined.

Materials and Methods

An experiment to evaluate Wyoming big sagebrush control with metsulfuron and 2,4-D was established in 1982 and 1983 near Bloomfield and Questa, New Mexico. Both sites supported dense sagebrush stands with greater than 18% canopy cover and 13,000 plants/ha. The Bloomfield site was established on a deep and well drained Doak sandy loam (Typic Haplagnid). Five composite soil samples collected to 10-cm depth in the immediate area of the experiment contained 86% sand, 12% silt and 2% clay, with 1.6% organic matter and a pH of 7.0. Slope at the site was 1 to 3% and elevation was 1,600 m. Prominent grasses included blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.), galleta (*Hilaria jamesii* [Torr.] Benth.), sand dropseed (*Sporobolus cryptandrus* [Torr.] Gray), and squirreltail (*Elymus longifolius* (Smith) Gould). The Questa site was established on a Fernando loam soil (Ustollie Haplagnid) containing 65% sand, 26% silt and 9% clay with 1.3%

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Appreciation is expressed to Norman Wolf, San Juan County Extension agent, to Dupont Chemical Company for herbicide, and to the Farmington and Taos Resource Area BLM for their assistance in the research. Financial support was provided by the New Mexico Range Improvement Task Force, the New Mexico Agricultural Experiment Station, and the Integrated Pest Management Special Grants Program.

Journal Article 1572 of the New Mexico Agr. Exp. Sta., Las Cruces 88003-0003.

Manuscript accepted 1 May 1991.

organic matter and a pH of 6.5. Average slope was 1 to 3% and elevation was 2,150 m. Common grasses included western wheatgrass (*Agropyron smithii* Rydb.), galleta, and blue grama.

Initial treatments were applied to Wyoming big sagebrush during the period of primary shoot growth on 19 May, 10 June, and 30 June 1982. Treatments included a 60% active ingredient, dry, flowable formulation of metsulfuron at 0.14, 0.28, and 0.56 kg ai/ha; and the butoxyethyl ester and alkanolamine salt of 2,4-D at 2.2 kg ae/ha. Treatments were reapplied to a nearby set of plots on 8 June 1983, except metsulfuron rates were reduced to 0.035, 0.07, and 0.14 kg/ha, and only 2,4-D ester was applied at 2.2 kg/ha. Precipitation was above normal during both years of herbicide applications at Bloomfield (Table 1) and Questa (data not shown).

Table 1. Precipitation recorded at Otis, New Mexico, near the Bloomfield site between 1982 to 1988.

Month	50-year average	Precipitation by year					
		1982	1983	1984	1985	1986	1987
(mm)							
January	15	11	41	6	22	0	24
February	11	31	9	1	7	13	40
March	17	34	34	17	36	9	25
April	14	4	10	11	75	29	3
May	10	47	8	5	1	14	13
June	7	0	10	17	6	34	9
July	24	42	14	45	68	70	11
August	32	93	65	64	1	46	15
September	21	22	47	19	41	49	12
October	29	2	24	46	39	49	22
November	16	15	23	7	23	78	40
December	15	51	36	17	5	16	14
Total	211	352	321	255	324	407	228
							301

Herbicides were applied with a trailer-mounted sprayer (6.4 m boom) delivering 140 l/ha total volume. The 2,4-D formulations were mixed in water or in a water-plus-diesel mixture (1:9 v/v). Metsulfuron was mixed in water only. A 0.5% (v/v) surfactant (trimethylnonyl-polyethoxy-ethanol) was added to all mixtures. Plots were 19.2 by 67 m and replicated in a randomized complete block design. Wyoming big sagebrush mortality was determined by counting live and dead plants before and 3 growing seasons (about 28 months) after treatment. Counts were made within two 1-m by 35-m belt transects located diagonally across each plot. Wyoming big sagebrush canopy cover was also measured before and 3 growing seasons after treatment along two 35-m line intercept transects placed in each plot (Hutchings and Pase 1963).

Grass and forb yield was determined from 1982 treatments by harvesting species in 2,4-D ester, metsulfuron, and untreated plots. Herbage data was collected in August 1982, 1983, 1985, and 1989 at the Bloomfield site, and all dates except 1989 at Questa because this area was disturbed. Data were obtained by clipping species within 10 randomly located 0.25-m² quadrats in each plot. Cattle grazed both study sites lightly in winter, but neither area was grazed during the summer growing season throughout the study.

A second experiment was established near earlier treatments on the Bloomfield site to evaluate spring and fall applications for control using metsulfuron and 2,4-D in 1986 and 1987. Treatments consisted of 2,4-D ester at 2.2 kg/ha, metsulfuron at 0.07 kg/ha, and a mixture of 2,4-D at 1.1 kg/ha and metsulfuron at 0.035 kg/ha. Treatments were replicated 3 times and applied to the same sized plots, and in the same manner as previously described, during Wyoming big sagebrush primary shoot growth (14 May, 13 June 1986; 25 April, 11 May, and 13 June 1987) or during the flowering and fruiting growth stages (23 September, 18 October 1986, 19 September, and 17 October 1987). Wyoming big sagebrush mortal-

ity and canopy reduction data was collected for all treatments using the same procedures described in the previous experiment. Within untreated (control) plots, 30 Wyoming big sagebrush plants were randomly selected for monthly shoot elongation measurements beginning in mid-March and continuing to mid-November 1986. Measurements were repeated for the same period in 1987 as an index to predict susceptibility of Wyoming big sagebrush to the herbicides. Four terminal shoots on each plant were permanently marked at a prominent node with color-coded wire, at or near the 4 cardinal directions on the outer canopy perimeter. Measurements of current year growth were taken from the marked node to the apex of the shoot. As flowering shoots developed in mid-summer, they were marked for separate measurement from vegetative shoots. On each sample date, sagebrush phenology was also recorded using a numerical system described by DePuit and Caldwell (1973). Precipitation on the study area was nearly twice the 50-year average in 1986, although winter rainfall (Dec. 1985–March 1986) previous to herbicide application was slightly below normal (Table 1). Precipitation was near the long-time average in 1987, but fall-winter precipitation was above average.

A third experiment to evaluate additional rates of metsulfuron applied in spring or fall was established in mid-May 1987 and 1988, and early October 1987 and 1988 at the Bloomfield site. Treatments included metsulfuron at 0.0175, 0.035, 0.07, 0.14, 0.28, and 0.56 kg/ha. Metsulfuron was applied with a pressurized CO₂ backpack sprayer for product explosion at 20 psi through a 2.5-m boom. Walking speed was timed to assure uniform application of treatments. Plot size was 9-m by 15-m with 3 replications. Wyoming big sagebrush mortality was determined in each plot in August 1990 using two 1-m by 15-m belt transects. Mortality results from this experiment were pooled with similar data acquired from other metsulfuron treatments applied at the Bloomfield site between 1982 and 1988 to show the relative effectiveness of the herbicide by rate and season applied. Metsulfuron treatments applied during this period in April, May, or June were combined as a spring data set, whereas treatments applied in September or October were combined as a fall data set. Separate regression analyses were conducted on spring and fall data sets to relate metsulfuron rates to Wyoming big sagebrush mortality.

Statistical Analysis

Apparent sagebrush mortality and canopy reduction means (\bar{x}) for each experiment were transformed to the arc sin \sqrt{x} , and subjected to analysis of variance using the protected LSD technique (Statistical Analysis System 1982). Herbage yield data did not differ significantly ($P > 0.05$) by date of herbicide application, so values were pooled within years by treatment for analysis.

Results and Discussion

Wyoming Big Sagebrush Control

Sprays of 2,4-D amine mixed in water or a diesel oil:water emulsion were less efficacious than 2,4-D ester, killing less than 15% of the Wyoming big sagebrush when applied in 1982 near Bloomfield and Questa, N.M. (data not shown). This agrees with numerous studies that have reported the advantage of ester formulations of 2,4-D compared to amines for sagebrush control (Evans et al. 1979). Also, no differences were found when 2,4-D ester was mixed in a 1:9 diesel oil:water carrier or mixed in water only for Wyoming big sagebrush control. Use of a diesel oil:water emulsion is usually recommended to reduce evaporation potential when aerially applying 2,4-D, and to increase herbicide absorption (Scifres 1980). As expected, 2,4-D ester killed a higher percentage of Wyoming big sagebrush when applied earlier in spring than later in the season (Table 2). However, Wyoming big sagebrush mortality

Table 2. Wyoming big sagebrush mortality and canopy reduction 3 years after ground application of herbicides in May-June, 1982 near Bloomfield and Questa, New Mexico.

Herbicide	Rate ¹	Sagebrush response by application date					
		Bloomfield		Questa			
(kg/ha)	5/19	6/10	6/29	5/18	6/11	6/30	
2,4-D ester ³	2.2	37	14	18	38	25	27
Metsulfuron	0.14	48	52	54	70	64	58
Metsulfuron	0.28	83	73	70	69	78	87
Metsulfuron	0.56	90	90	90	87	90	77
		(% mortality) ²					
		(% canopy reduction)					
2,4-D ester	2.2	28	8	15	25	13	21
Metsulfuron	0.14	48	35	35	80	67	45
Metsulfuron	0.28	90	80	73	67	94	90
Metsulfuron	0.56	98	94	98	94	90	80

¹Expressed as acid equivalent for 2,4-D; and as active ingredient for metsulfuron.

²LSD (0.05) values for comparing sagebrush mortality and canopy reduction values are 14 and 16, respectively.

³No significant difference was found between mixing 2,4-D ester in a 1:9 diesel oil water carrier or mixing the herbicide in water only, thus, data from these treatments were pooled for analyses.

never exceeded 38% on any spray date at either location, and these percentages are low in comparison to those usually reported when the plant is sprayed in more mesic environments (Evans and Young 1977).

Wyoming big sagebrush leaves had mostly shed 4 months after 2,4-D applications, but were only discolored and remained on shrubs sprayed with metsulfuron (data not shown). After 1 year, about 75 to 95% of the leaves were shed from plants sprayed with metsulfuron, but some green tissue remained on most plants. Wyoming big sagebrush mortality 3 years after applying metsulfuron at 0.14 kg/ha was greater across spray dates at the Questa location (64%) compared to Bloomfield (51%) (Table 2). Annual rainfall is normally 10 cm higher near the Questa site compared to Bloomfield and, although soil moisture was high at both locations when plants were sprayed, we suspect environmental conditions were more favorable for Wyoming big sagebrush growth near Questa. Metsulfuron was equally efficacious at higher rates of application across locations and spray dates, averaging 77 and 87% at 0.28 and 0.56 kg/ha, respectively. Wyoming big sagebrush mortality after applying lower rates of metsulfuron on 8 June 1983 was comparable across sites, and averaged 31, 44, and 60% at rates of 0.035, 0.07, and 0.14 kg/ha, respectively. Canopy reduction 3 growing seasons after 1983 treatments averaged 35, 59, and 78%, respectively. Mortality with 2,4-D ester averaged 35% and canopy reduction averaged 33%.

Typically, Wyoming big sagebrush is senescent from early November until bud break in late March to early April in northern New Mexico. Spring shoot growth follows bud break by 2 to 4 weeks in late April and continues until mid-September. Flowering and fruiting occurs mostly in October and November. Phenophasic beginnings were generally later (by 2 to 4 weeks) in 1986 than those observed in 1987 (Anderson 1989). DePuit and Caldwell (1973) reported main phenophasic beginnings to be about a month later on Wyoming big sagebrush in northern Utah compared to plants we examined in this study. Growth of Wyoming big sagebrush terminal shoots in 1986 was greatest between 15 April and 15 May (Fig. 1). Mean shoot length for this month averaged about 11 mm, with a range from 0 to 72 mm. Zero was the mode and the median was 7 mm. This large variation was typical for all measurement periods because terminal shoot growth within and between plants was highly erratic. About 20% of marked shoots exhibited no growth during the entire year. Shoot growth was

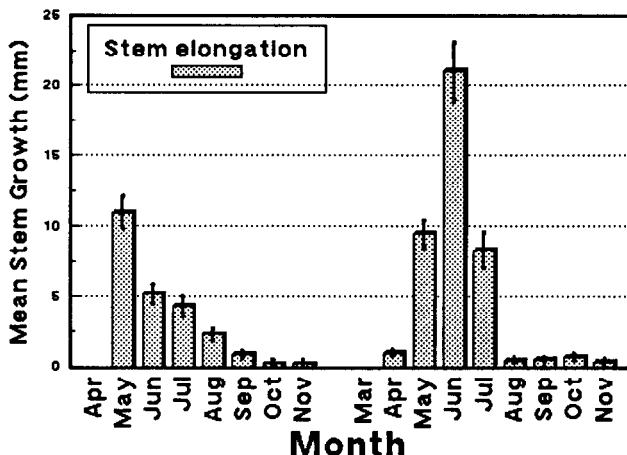


Fig. 1. Mean monthly growth increment and standard error measured on 120 Wyoming big sagebrush shoots in 1986 and 1987 at the Bloomfield site.

above-average on some plants, but no growth was observed on other shoots on the same plant. Lack of uniform shoot growth was probably responsible for the poor Wyoming big sagebrush control (11% average mortality) by 2,4-D ester at 2.2 kg/ha in 1986 (Table 3). Activity of metsulfuron at 0.035 kg/ha was also poor when applied in May and June (23% average mortality), but control was greater when applied in September and October (55% average mortality).

Table 3. Wyoming big sagebrush mortality and canopy reduction in August 1990 following application of herbicides in 1986 and 1987 near Bloomfield, New Mexico.

Herbicide	Rate	Year	Sagebrush response by application date				
			(kg/ha)	(% mortality)			
2,4-D ester	2.2	1986	—	13	10	13	7
		1987	68	45	25	13	46
Metsulfuron	0.035	1986	—	25	22	57	53
		1987	26	27	17	63	63
2,4-D + Metsulfuron	1.12+ 0.0175	1986	—	18	15	33	48
		1987	55	48	17	67	74
2,4-D ester	2.2	1986	—	18	17	25	12
		1987	65	48	17	10	45
Metsulfuron	0.035	1986	—	37	32	72	70
		1987	33	32	20	62	73
2,4-D + Metsulfuron	1.12+ 0.0175	1986	—	28	23	48	62
		1987	48	52	13	60	85

¹LSD (0.05) values for comparing sagebrush mortality and canopy reduction are 25 and 27, respectively.

Terminal shoot measurements were again highly variable in 1987, except that average cumulative growth was greater than that observed in 1986 (43.3 compared to 23.9 mm, respectively) (Fig. 1). Growth measurements included vegetative shoots and flowering stalks, which usually could not be distinguished until mid-July or August. Mean growth of shoots on which flowering later occurred was nearly 4 times greater than that of shoots, which did not produce flowers in either year (data not shown). A higher percentage of Wyoming big sagebrush was killed or defoliated in 1987 when 2,4-D was applied on early or late application dates (April, May, and October) compared to dates near the middle of the growing season (June and September) (Table 3). Greater effective-

ness of 2,4-D for control of sagebrush in spring and fall, compared to summer months, agrees with other studies by Hyder (1954) and Evans et al. (1979). As was observed in 1986, metsulfuron applied in 1987 killed a higher percentage of Wyoming big sagebrush during later application dates (average 59% mortality for September and October), than for earlier dates (average 23% mortality for April, May, and June). McDaniel and Duncan (1987) reported a similar seasonal difference in the effectiveness of metsulfuron for control of broom snakeweed. Treatments that included metsulfuron at 0.0175 kg/ha plus 2,4-D at 1.1 kg/ha provided comparable Wyoming big sagebrush control to 2,4-D alone at 2.2 kg/ha in April and May, and to metsulfuron alone at 0.035 kg/ha in September and October. These data suggest synergism may exist between these 2 herbicides for Wyoming big sagebrush control but the optimum combination rates are unknown.

Metsulfuron applied at various rates in 1987 and 1988 further substantiated that the herbicide is more efficacious for Wyoming big sagebrush when applied in fall compared to spring (Table 4).

Table 4. Mortality of Wyoming big sagebrush following applications of metsulfuron in May and October 1987 and 1988 near Bloomfield, New Mexico.

Metsulfuron rate (kg/ha)	Sagebrush response by season of application	
	Spring (%)	Fall (%)
0.0175	22 ^a	40 ^d
0.0350	47 ^d	72 ^c
0.07	70 ^c	88 ^b
0.14	74 ^c	94 ^{ab}
0.28	100 ^a	98 ^a
0.56	90 ^{ab}	100 ^a

^aMeans followed by a different letter are significantly different by LSD at the 0.05 level.

Metsulfuron was nearly twice as effective at lower rates when applied in the fall compared to spring. As expected, when data from all metsulfuron treatments applied at the Bloomfield location between 1982 to 1988 were combined into spring and fall data sets, Wyoming big sagebrush mortality increased as rates increased (Fig 2). Further research is needed to explain the physiological basis for the greater metsulfuron activity on Wyoming big sagebrush applied in fall compared to other times of the year.

Forage Production

Total herbaceous production, as end-of-season standing crop, was not significantly different in herbicide-treated plots compared to untreated rangeland the first growing season after application near Questa, but was 200 to 300% higher in sprayed areas near Bloomfield (Table 5). Total herbaceous standing crop usually

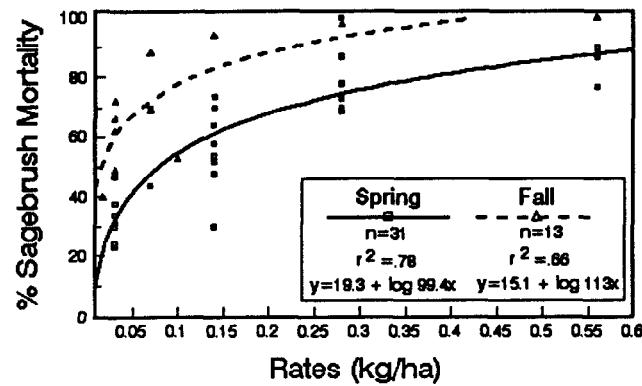


Fig. 2. Wyoming big sagebrush mortality following application of various rates of metsulfuron in spring (April, May, or June) and fall (September or October) near Bloomfield, New Mexico, 1982 to 1988.

increased on all treated plots, compared to untreated areas, at the Questa site after the second post-treatment growing season. In general, herbaceous yield in plots sprayed with 2,4-D and the 0.14 kg/ha rate of metsulfuron were equivalent. As expected, herbage yield was usually greater where a higher percentage of sagebrush was controlled by the 0.28 and 0.56 kg/ha rates of metsulfuron. Major differences among treatments were contributed by grasses, with galleta contributing about 65% of the total composition by weight at Bloomfield and western wheatgrass contributing about 85% at Questa. Blue grama was the most important associated species at both sites. No evidence of damage to any herbaceous species was noted in either 2,4-D or metsulfuron treatments after the first growing season. Broadleaf species, primarily woolly plantain (*Plantago patagonica* Jacq.) and scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.), were equally evident in either treated or untreated plots, but comprised less than 1% of the total composition by weight at both sites (data not shown).

Conclusions

Big sagebrush is successfully controlled by 2,4-D and other phenoxy herbicides in the Great Basin, Columbia River, and the northern High Plains. However, because results are erratic, this practice has not been widely employed on the Colorado Plateau encompassing portions of Arizona, Utah, Colorado, and New Mexico (West 1978). Wyoming big sagebrush is reportedly susceptible to 2,4-D when soil moisture is available to promote at least 5 to 7 cm of new shoot growth before spraying phenoxy herbicides (Cornelius and Graham 1958). However, precipitation averages about 6.5 cm on the Colorado Plateau from January to June,

Table 5. Herbaceous standing crop in August 1982, 1983, 1985, and 1989 following herbicide applications to Wyoming big sagebrush in May-June 1982 near Bloomfield and Questa, New Mexico.

Location	Herbicide	Rate (kg/ha)	Standing crop by year (kg/ha)											
			1982	1983	1985	1989	1982	1983	1985	1989	1982	1983	1985	1989
Bloomfield	Control		172 ^c	160 ^c	159 ^b	160 ^b	64 ^c	65 ^b	112 ^b	92 ^b	250 ^c	236 ^c	284 ^c	284 ^b
	2,4-D ester	2.2	194 ^c	298 ^b	208 ^b	362 ^a	168 ^b	107 ^a	173 ^a	178 ^{ab}	434 ^b	430 ^b	391 ^b	622 ^a
	Metsulfuron	0.14	264 ^{bc}	341 ^{ab}	267 ^b	292 ^{ab}	202 ^b	136 ^a	224 ^a	194 ^{ab}	477 ^b	485 ^{ab}	518 ^a	532 ^a
	Metsulfuron	0.28	379 ^{ab}	446 ^a	432 ^a	418 ^a	358 ^a	106 ^a	165 ^{ab}	200 ^a	791 ^a	602 ^a	630 ^a	670 ^a
	Metsulfuron	0.56	490 ^a	441 ^a	389 ^a	430 ^a	174 ^b	142 ^a	211 ^a	164 ^{ab}	703 ^a	592 ^a	626 ^a	678 ^a
Questa	(Western wheatgrass)												(Blue grama)	
	Control		85 ^b	137 ^c	108 ^c	—	1 ^a	60 ^{ab}	30 ^b	—	146 ^a	255 ^c	195 ^d	—
	2,4-D ester	2.2	205 ^a	384 ^b	279 ^{bc}	—	26 ^a	85 ^{ab}	51 ^b	—	231 ^a	562 ^{ab}	367 ^c	—
	Metsulfuron	0.14	55 ^b	236 ^{bc}	474 ^b	—	39 ^a	105 ^a	237 ^a	—	104 ^a	353 ^{bc}	753 ^b	—
	Metsulfuron	0.28	68 ^b	670 ^a	820 ^a	—	15 ^a	44 ^b	66 ^b	—	83 ^a	750	932 ^{ab}	—
	Metsulfuron	0.56	120 ^b	568 ^a	1157 ^a	—	15 ^a	24 ^b	66 ^b	—	135 ^a	653 ^a	1330 ^a	—

^aNumbers in the same column and location followed by the same letter are not significantly different by LSD at the 0.05 level.

which is probably not enough to promote adequate shoot growth in most years to insure effective Wyoming big sagebrush control. Our data suggest, even in years with above average winter-spring precipitation, terminal shoot growth is likely to average less than 5 cm, and growth among stems is likely to be highly variable within and between plants.

Metsulfuron activity does not appear to be related to leaf or leader growth because Wyoming big sagebrush was more readily controlled by the herbicide when applied at comparable rates in fall compared to spring. Wyoming big sagebrush control averaged 65% when metsulfuron was fall-applied at 0.035 kg/ha, whereas mortality increased to 88% when metsulfuron was sprayed at 0.07 kg/ha. Metsulfuron plus 2,4-D worked reasonably well at the one combination rate examined. Some synergism may exist, but further research is needed to determine optimum metsulfuron plus 2,4-D combinations.

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Technical Notes

Surgical establishment of esophageal fistulae in suckling calves

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Abstract

Esophageal fistulae were established in five 34-day-old suckling calves by a modified surgical procedure used previously for sheep and goats. After skin incision, the esophagus was exposed by separating the brachiocephalicus and sternocephalicus muscles. A cannula was inserted into the esophagus after a longitudinal incision was made into the lumen of the esophagus. Sutures were not used in the esophagus. The calves recovered quickly with moderate post-operative swelling. We concluded that the surgical procedure was satisfactory and that diets were collected readily and without fistulae shrinkage.

Key Words: beef cattle, pasture, rangeland, cattle diets

Esophageally fistulated animals have been utilized extensively to obtain a sample of the grazing ruminant's diet (Lesperance et al. 1974, Cohen 1979, Samuel and Howard 1982, Hart et al. 1983). Several authors have described surgical techniques for establishing esophageal fistulae in mature ruminants (Van Dyne and Torell 1964, Bishop and Forseth 1970, Little and Tokken 1970, Pfister et al. 1990). Only limited information concerning diets of suckling calves has been published (Horn et al. 1979, Peischel 1980, Ansotegui 1986) and procedures for establishing esophageal fistulae in the suckling calf have not been published. Our objective was to test the suitability of a simplified method for establishing esophageal fistulae in sheep and goats (Pfister et al. 1990) for young suckling calves.

Materials and Methods

Esophageal-fistulae were established in 5 suckling beef calves (average age = 34 days; average body weight = 65 kg) with modification of the procedure described by Pfister et al. (1990) for sheep and goats. Calves were separated from their dam 12 hours before surgery. Each calf was given a .1 ml intramuscular injection of xylazine (Rompun¹). The calf was placed in right lateral recumbency on a surgical table and hair was closely clipped with a number 40 clipper from the left lateral neck region caudal to the jaw to the cranial shoulder region and from the top of the neck to just across the midline ventrally. The surgical area was scrubbed with soap and with betadine surgical scrub²; then the surgical area was rinsed with a 70% alcohol solution. The surgical site (the junction between the brachiocephalicus and sternocephalicus muscles and 30 to 40 mm posterior to the midpoint between the jaw and shoulder) was anesthetized using 20 ml of a 2.5% (volume × volume) procaine solution. The local anesthetic was injected sub-

cutaneously and into underlying muscles dorsal and cranial to the incision site in an inverted L shape. A 9.5 mm diameter tygon tubing was passed down the esophagus to the point of just caudal to the proposed incision site. A 60 mm longitudinal skin incision was made overlying the brachiocephalicus and sternocephalicus muscles. The brachiocephalicus and sternocephalicus muscles were separated by blunt dissection, and the aid of the intraluminally placed tygon tubing, the esophagus was located and exposed. A 60 mm longitudinal incision was made into the lumen of the esophagus. The incised edges of the mucous membrane of the esophagus were grasped with Allis forceps to avoid slippage of the mucous membrane away from the incision site. The tygon tube was then removed. A convex 89 mm × 25.4 mm polyethylene coated aluminum cannula³ with a 65-mm threaded shank measuring 6.35 mm in diameter was inserted into the lumen of the esophagus. A stopper or plug was fabricated by gluing the small end of a #7 rubber stopper to the large end of a #6 stopper. The 2 stoppers were wrapped with black electricians tape and a 6.45 mm hole was bored through the center of the 2 stoppers. Dimensions of the stopper were 38.1 mm and 25.4 mm diameter for the large and small ends respectively and 50.8 mm in length. The shank was put through the stopper and was secured with a wing nut. The esophagus was not sutured. In 3 of the 5 calves, a single suture through the skin was required cranial or caudal in the skin incision to insure a tight fit around the stopper. The incision site was then lavaged with 20 ml of penicillin and dihydrostreptomycin (combiotic⁴) and an intramuscular dose of 10 ml of combiotic was administered.

The procedure required about 20 minutes and calves were able to stand and walk immediately after surgery. The surgical site was observed daily for any signs of infection and skin sutures were removed 12 to 14 days after surgery. Each calf was given 10 ml of combiotic daily for 5 days after surgery. The cannula was first removed and rotated about 4 weeks after surgery. The fistula was fully healed and there was no sign of soreness resulting from the cannula.

A vinyl bag with a 178 mm × 152 mm mesh bottom with sides and ends measuring 229 mm and 130 mm high, respectively was constructed for collection of esophageal extrusa. The bag was attached with neck and girth straps as described by Kartchner and Adams (1983).

Esophageal extrusa was collected on 15 June (average calf age = 115 days), 26 July, 20 September, and 29 November from the 5 suckling calves on rangeland. Cows with the suckling calves were penned with water but not given access to feed at 1600 h the day before collections were made and collections were made the following morning at 0700 h. The collection periods lasted from 20 to 30 minutes.

Results and Discussion

The surgical technique for the suckling calves was found to be effective with only moderate post-operative swelling. The milk diets consumed by the calves were ideal for recovery. Post-

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Publication has been approved by the director of the Montana Agr. Exp. Sta., Journal Ser. 2519.

This paper is a contribution from the USDA, Agriculture Research Service, the University of Nebraska, and the Montana Agricultural Experiment Station. Mention of a trade name or product does not constitute a recommendation or endorsement for use by the USDA.

Manuscript accepted 16 December 1990.

¹Haver-Vayvet Div. Miles Laboratories, Inc., Shawnee, Kansas 66201.

²Schering Corporation, Animal Health Division, Kenilworth, New Jersey 07033.

³Cannula manufactured by Precision Machine, 2933 North 36th Street, Lincoln, Nebraska 68504.

⁴Pfizer Inc., New York, New York 10017.

operative difficulties were not observed for suckling, blockage of the esophagus, or milk leakage from the fistula.

Diets could have been collected earlier than 115 days of age; but a severe drought slowed forage growth and collections were delayed. The procedure of penning the cows and calves overnight was particularly effective, as all animals began grazing immediately when turned out for collection. This was a concern because the cows were not accustomed to being handled. No problems with fistulae shrinkage or in replacing esophageal cannulae after a 30-minute collection period were encountered.

We concluded that this esophageal surgical technique was satisfactory for use in suckling calves. The calves required minimal post-operative care and forage collection was done easily without esophageal fistulae shrinkage.

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Book Reviews

Ecosystems of Florida. Edited by Ronald L. Myers and John J. Ewel, with 30 text contributors. 1990. University of Central Florida Press, Orlando. Available through University Presses of Florida, Gainesville. 765p. US\$75.00 cloth, US\$29.95 paper. ISBN 0-8130-1012-8, 0-1830-1022-5, respectively.

Everyone will find something of interest in *Ecosystems of Florida*, a new comprehensive survey of the state's natural resources. Eighteen chapters cover the great natural diversity of Florida's ecosystems, and the fascinating components which contribute to them.

The book has five major sections which focus on (1) historical, physical, and biological geography, (2) upland ecosystems, (3) freshwater and aquatic ecosystems, (4) coastal ecosystems, and (5) prospects and strategies for conservation. Most of the information related directly to range management can be found in the first eight chapters. There is considerable discussion of the ecology and management of herbaceous species found in the dry and wet prairies and in the different forest types. Discussions of management emphasize strategies for preservation and conservation more than use. The book contains next to nothing on the role of domestic livestock in management of the plant communities. Cattle (a word not found in an otherwise detailed index), which are abundant in the state, are treated as a threat to the upland areas and not as a tool. All this disparagement by omission and casual insult is unfortunate because the real threats to Florida ecosystems come directly from demands of a large and growing suburban population, from real estate development, from introductions of exotic species, and from intensive agriculture. That livestock receive little attention indicates the momentum (= mass \times velocity) of these other threats in Florida. The descriptions of the upland plant communities are detailed, but enjoyably readable.

But if you are not interested in the upland ecosystems, the book continues with chapters on swamps, freshwater marshes (including the Everglades), lakes, rivers and springs, dunes and maritime forests, salt marshes, mangroves, inshore marine habitats, and coral reefs. Throughout, the discussions are scientifically detailed, but the pace is relaxed and the reading is interesting. At times, it helps to have a good knowledge of Florida geography. Many chapters contain discussions of relevant Florida history.

Threatened wildlife species are discussed, including such well-publicized species as the West Indian manatee and the Florida panther. Appropriately, emphasis is on conservation of entire habitats or the entire ecosystems. These discussions are carried out with ecological concern and scientific detail, without the depressing, repetitive warnings of many books and television programs.

The text is salted with good quality black-and-white photographs, some of them taken specifically for the book. The early chapters contain several good historical photographs. Included are some informative maps in the text, some tables, and a few figures. As enjoyable as it is to read, *Ecosystems of Florida* will be hugely valuable as a reference; it contains ninety-seven pages of references, a general index, an index of common names, and an index of scientific names. The \$75 issue is wonderfully clothbound and printed on good quality paper.

I am sure the editors think that every interested citizen of the state of Florida should have a copy of this book, and they are probably right. It is an excellent, enjoyable book for anyone interested in ecological work or issues. If you have considered moving

or retiring to Florida, you should ignore those glossy, colorful tourist books and get this one instead. The book will enhance your knowledge and appreciation of the state.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

The Grazing Land Ecosystems of the African Sahel. By Henry Noël Le Houérou. 1989. Springer-Verlag, New York. 282 p. US\$89.50 hardbound. ISBN 0-387-50791-4.

This volume, number 75 in the familiar green-bound Ecological Studies Series, is an overview of the ecology of the Sahel region of Africa. The Sahel extends from the Atlantic Ocean to the Red Sea, and is sandwiched between the Sahara Desert to its north and the "Sudanian" savannas to its south. The region has in the past 30 years shown steady increases in human population and livestock numbers. The area has seen desertification from the north, destructive cultivation from the south, and the extermination or near extermination of most wildlife populations region wide.

The book consists of 8 chapters entitled (1) Definitions, geographic limits, contacts with other ecoclimatic zones, (2) Environmental characteristics, (3) Flora and vegetation, (4) Wildlife, (5) Livestock, (6) Development outlook: constraints and limits, (7) Monitoring: a case study, the Ferlo Region of northern Senegal, and (8) General conclusions: toward an ecological management of the Sahelian ecosystems. Following Chapter 8 is a large list of references, a reasonably detailed general index, and an index of scientific names. The book contains 6 black-and-white photographs and a disproportionately large number of tables and figures, which collectively make up at least half of its length.

The text of the book is terse and direct throughout. It is sometimes fragmented by the large number of tables and figures which often cover a number of successive pages. In places the text seems more like scaffolding surrounding the tables and figures, an effect hardly redundant, because many captions are informationally minimal. In places, especially in Chapter 2, the text contains more ecological and climatic jargon than is necessary. Overall though, the level of precision in terminology is consistently high, even when the jargon is absent. Many acronyms are used. Fortunately, an index of them is included at the beginning of the book.

Neither preface nor introduction is present to name the audience of the book. Individuals involved in development projects in the Sahel would no doubt find it useful. In particular, those developing proposals for research or development projects there would be able to use the tabular data in the book to advantage. While the text is readable enough, the book's greatest value will be as a reference. The tables and figures contain regional data from the author's work and from other investigations. Individuals involved with aerial surveys and remote sensing of other kinds will find the chapter on comprehensive monitoring in the Ferlo region of particular interest. It contains some practical discussions of common technical methods available in remote sensing. Researchers and practitioners of agroforestry will find some general information on systems existing in the Sahel.

For those who read the entire book, the message is deafeningly understated. Those damnable statistics on population growth, agricultural development, livestock numbers, and wildlife numbers have been and still are stalking the Sahel. In the most general terms, the author briefly explains the kinds of political, sociological, and economic transformations which are needed to develop ecologically based management for the region. No dramatic pleas of urgency are present or needed. The numbers speak well for themselves.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

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Journal of Range Management

**Official bimonthly publication of
Society for Range Management**

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