Journal of Range Management

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Invited Synthesis Paper:

Coyote depredation control: An interface between biology and management

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Abstract

Predation by coyotes (*Canis latrans*) on livestock continues to plague producers in the United States. Agricultural interests are concerned about coyote predation because sheep inventories in the U.S.have declined >85% in the past 60 years, with a 25% decline between 1991 and 1996. This decline in sheep numbers has been attributed to low economic returns among producers, with coyote predation cited as a major causative factor. Generalizations about the magnitude and nature of depredations can be misleading because of the varied nature of sheep operations, including size of operations, differences in management, and environmental circumstances surrounding individual operations. Coyote depredation rates appear to be influenced by sheep management practices, coyote biology and behavior, environmental factors, and depredation management programs. Most nonlethal depredation control techniques fall within the operational purview of the producers. The major controversy regarding depredation management focuses on programs that remove coyotes to prevent or curtail predation on domestic stock, especially on public lands. Differences in the magnitude, nature, and history of problems caused by coyotes, as well as the circumstances in which they occur, dictates a need for a variety of techniques and programs to resolve problems. The resolution of coyote depredation upon livestock remains controversial for producers, resource managers, and the general public. Because various segments of society attach different values to coyotes, resolution of depredations should use management programs that integrate the social, legal, economic, and biological aspects of the animals and the problem. Preferred solutions should involve procedures that solve problems as effectively, efficiently, and economically as possible in the least intrusive and most benign ways. Predation management requires a partnership among producers and wildlife managers to tailor programs to specific damage situations so the most appropriate techniques can be selected. This paper attempts to clarify the issues surrounding depredation management, synthesize past and current research, and provide information to resource managers associated with coyote depredation management. This synthesis integrates current understandings of coyote biology and behavior, the nature of depredations upon sheep producing enterprises, and the merits of various depredation control strategies and techniques.

Key Words: coyote, *Canis latrans*, domestic livestock, predation, management

Control of mammalian predators to protect livestock or enhance game populations has been practiced worldwide for centuries. Manipulation of canid populations, especially reduction of red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), wolves (*C. lupus*), jackals (*C. mesomelas*, *C. aureus*), and dingos (*C. familiaris dingo*), has occurred both historically and currently with mixed results (Harris and Saunders 1993, Reynolds and Tapper 1996). Some canid removal is used as a conservation tool to assist recovery of threatened or endangered species in areas where predators are non-native or overabundant (Garrott et al. 1993). With the popularization of carnivores and establishment of canid populations in the United States, with particular reference to the continued expansion of coyotes (Hilton 1978, Hill et al. 1987, Moore and Parker 1992) and successful reintroduction of wolves (Phillips et al. 1995, Bangs and Fritts 1996), managing conflicts between predators, livestock, and game populations is re-emerging as an issue for resource managers, biologists, and the general public (Mech 1996).

The coyote is one of the most successful, opportunistic, and widely distributed predators in North America (Bekoff and Wells 1986). Predation upon domestic livestock by coyotes is a widespread problem for producers throughout North America (Gier 1968, U.S. Fish and Wildlife Service 1978, Wade 1978, Andelt 1987). Techniques are available to reduce coyote depredations on livestock (Sterner and Shumake 1978, Wade 1978, Fall 1990), but the use of some control techniques and programs continues to be contentious and controversial (Buys 1975, Stuby et al. 1979, Kellert 1985, Andelt 1987, 1996). Many ideas, myths, and misperceptions about coyote depredation management exist; primarily questions regarding: what management techniques are available and effective; the effect of removal on coyote populations; and why is coyote predation on sheep a recurring problem with management programs currently in place? Recent studies of the efficacy of coyote management programs, relative effectiveness of various control measures, and the influence of management programs on coyote demographics suggest a need to synthesize some of these topics (see Andelt 1987, 1996 for reviews on coyote predation). We believe there is a need to address the controversy surrounding coyote depreda-

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Manuscript accepted 23 Apr. 1999.

tion management, to enlighten resource managers and the general public, and to stimulate discussion and research regarding new avenues of approaching the persistent problem of coyote depredation management. Through this paper, we attempt to synthesize the available information into a comprehensive interpretation and understanding of the relationships between coyote biology and depredation management. We discuss the current understandings of (1) coyote demographics, behavior, and population regulation, (2) the magnitude and factors influencing coyote depredations on livestock, and (3) the merits of various management strategies to alleviate coyote depredations on domestic livestock. We discuss the inter-relationships of the factors influencing coyote predation and management, and the need to understand the depredation issue as it relates to coyote behavior and biology. Our attempt is to provide a science-based perspective on the merits and pitfalls of coyote depredation management.

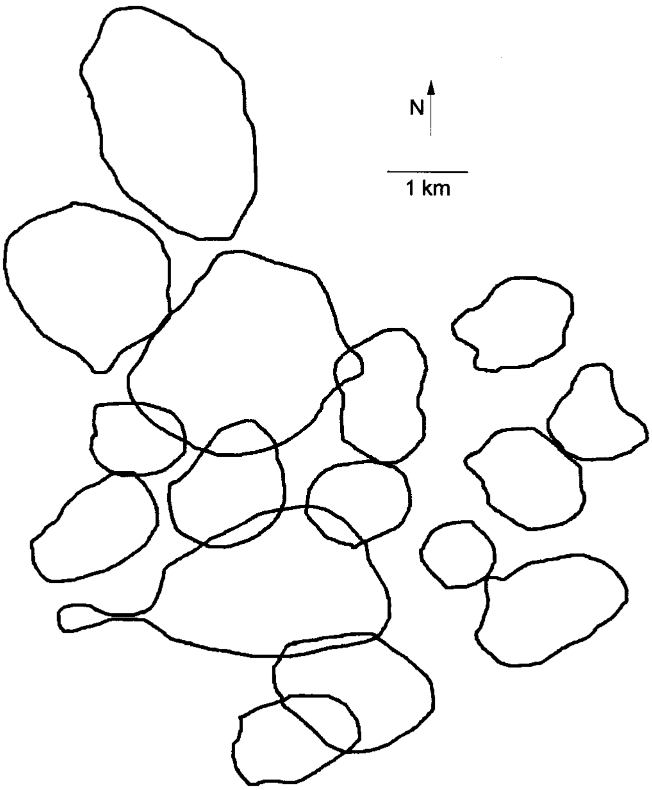

Fig. 1. Territorial boundaries of 16 female coyotes as determined by radiotelemetry locations, Webb County, Texas, 1984–1985 (adapted from Windberg and Knowlton 1988).

Coyote Demographics

Assessing the effect of management programs on coyote populations requires an understanding of the mechanisms and behaviors involved in regulating coyote demographic processes. Coyote demographics and population dynamics have been studied in many areas throughout the U.S. and Canada (e.g., Knowlton 1972, Nellis and Keith 1976, Andelt 1985, Windberg 1995). Coyotes are territorial with territories spaced contiguously across the landscape like pieces of a puzzle (Fig. 1; Bekoff and Wells 1986, Windberg and Knowlton 1988, Gese et al. 1989, 1996a, 1996b) with coyotes often times utilizing physical features, such as rivers and roads, to demarcate territory boundaries (Fig. 2). Each territory is controlled and maintained by a dominant alpha pair (Gese and Ruff 1997, 1998), with associated beta coyotes and pups (Camenzind 1978, Bekoff and Wells 1986, Gese et al. 1996a, 1996b). Pre-whelping pack size ranges from a pair of coyotes to 10 individuals (Gese et al. 1996a). Populations also include transient (Fig. 3) and dispersing individuals (Andelt 1985, Bekoff and Wells 1986, Gese et al. 1989, 1996a). Coyotes are monestrous (Kennelly and Johns 1976), with the dominant breeding pair producing a single litter per territory each spring; beta females may also produce offspring, but this rarely occurs (Gese et al. 1996a). Adults have relatively long reproductive lives (3–10 years) and produce average litters of 4 to 8 young. Because stable populations require that on average, breeding adults only recruit enough surviving offspring

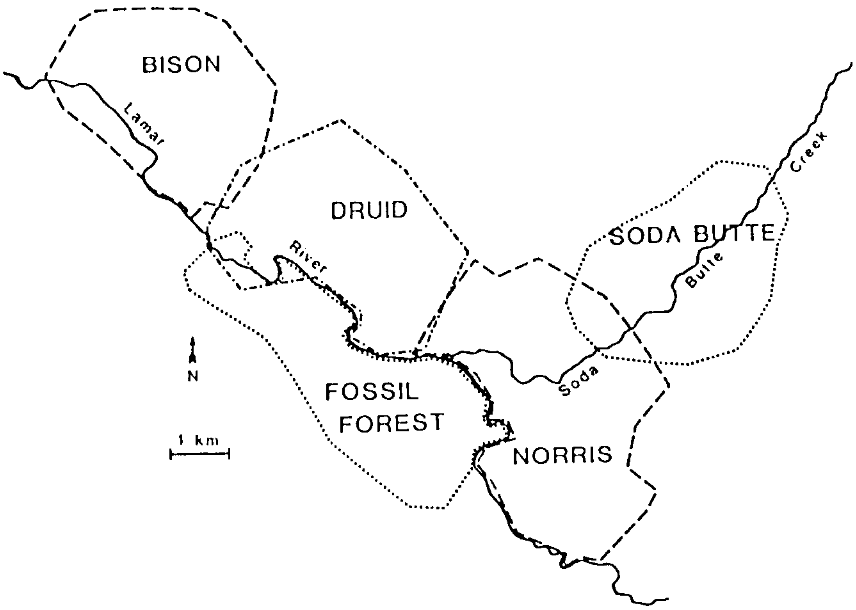

Fig. 2. Territorial boundaries of five resident coyote packs in the Lamar River Valley, Yellowstone National Park, Wyoming, winter of 1990–1991, as determined by visual locations (from Gese et al. 1996a, 1996b).

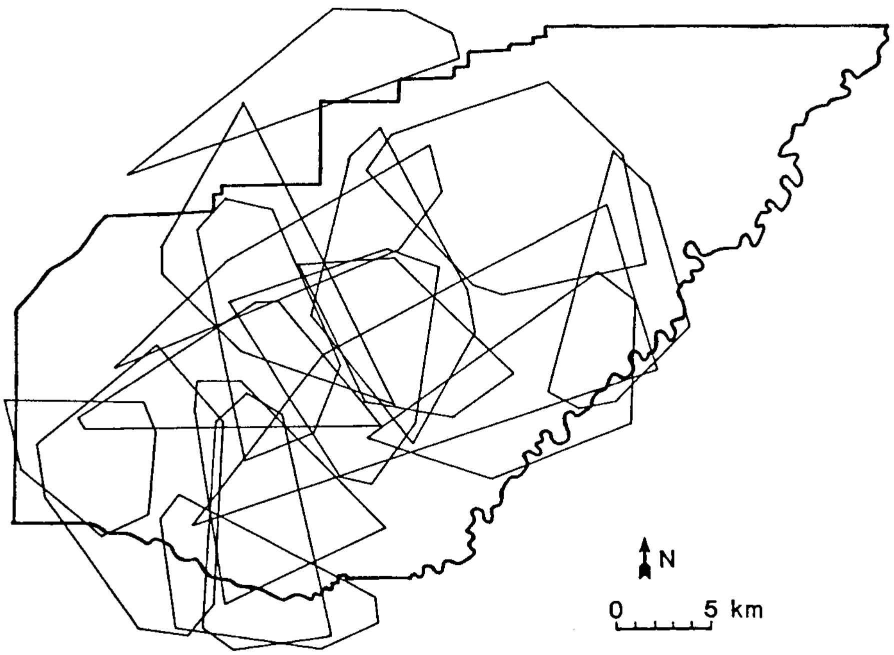

Fig. 3. Home range boundaries of 17 transient coyotes monitored on the Pinon Canyon Maneuver Site, Colorado, 1983-1987 (from Gese et al. 1988).

into the breeding population to replace themselves, less than 10% of the young from a given pair of coyotes need to survive and reproduce to maintain the population (assuming average reproductive lives of 4 years with litter sizes of 6 young). The other 90% die, disperse, or fail to reproduce. Hence population regulation is the interplay among the reproductive potential of coyotes and the opposing factors such as reproductive inhibition, mortality, and dispersal.

Factors Regulating Coyote Density

Estimates of coyote density range from 0.2 to 2.3 coyotes/km^2 with generally increasing densities from northern to southern U.S. Available food, especially in winter (Weaver 1979, Gese et al. 1996a), is the major factor regulating coyote abundance (Gier 1968, Clark 1972), mediated through social dominance and territoriality (Knowlton and Stoddart 1983, Gese et al. 1989, Knowlton and Gese 1995, Windberg 1995). Food abundance regulates coyote numbers by influencing reproduction, survival, dispersal, space-use patterns, and territory density (Gier 1968, Knowlton 1972, Todd et al. 1981, Todd and Keith 1983, Mills and Knowlton 1991, Gese et al. 1996a). Studies of coyote-lagomorph population cycles, where hares comprise a significant portion of the coyote diet, have demonstrated that during times when snowshoe hare (*Lepus americanus*) or black-tailed jackrabbit (*L. californicus*) numbers decline, coyote numbers decline (Clark 1972, Todd et al. 1981, Wagner 1981, Knowlton and Stoddart 1992, O'Donoghue et al. 1997). The mechanism for those declines was reduced ovulation rates and litter sizes, and a decrease in the percentage of adult and yearling coyotes that bred (Todd et al. 1981, Todd and Keith 1983). Food abundance also influences coyote numbers through its affect on dispersal of pups in winter (Gese et al. 1996a). In addition, food shortages can increase mortality rates, especially among juvenile coyotes (Windberg 1995). Human activities, particularly shooting, trapping, and vehicle collisions cause a high proportion of deaths of coyotes (juveniles and adults), including those in lightly exploited populations (Tzilkowski 1980, Davison 1980, Windberg et al. 1985, Gese et al. 1989, Windberg 1995). Crete and Lemieux (1996) hypothesized this could be a secondary effect related to competition for access to food. Coyote density (i.e., pack size and territory density) is also influenced by food abundance (Harrison 1992). In areas with rigorous winters, when carcass (carrion) biomass is low, coyote pack sizes remain small (Gese et al. 1996a, 1996b). In winters when carcass biomass is greater, more coyotes remain in their social group, and pack size and coyote density increase(Gese et al. 1996a, 1996b).

Food abundance also effects space-use patterns. Mills and Knowlton (1991) examined coyote territory sizes on 2 areas when prey abundance was high and later when it was low. In the Curlew Valley, Utah, coyote territory sizes increased during times of prey scarcity, while on the Idaho National Engineering Laboratory there was no change in territory size during a prey decline, but the percentage of transient coyotes increased. The higher exploitation rate (low adult survival) on the Curlew Valley site may have disrupted some of the "social traditions," allowing territorial adjustments that normally would not occur within short time frames. In addition, there is considerable variation in territory size among packs, presumably due to differences in habitat quality and prey base (Laundré and Keller 1984, Gese et al.1988).

Coyotes exhibit a dominance hierarchy within packs (Camenzind 1978, Gese et al. 1996a) and a land-tenure system of exclusive territories (Camenzind 1978, Bekoff and Wells 1980, 1986, Althoff and Gipson 1981, Bowen 1981, 1982, Messier and Barrette 1982, Andelt 1985, Windberg and Knowlton 1988, Gese et al. 1996a) which serve to mediate coyote numbers as social groups partition the landscape in relation to available habitat and food resources (Knowlton and Stoddart 1983, Gese et al. 1988, Knowlton and Gese 1995). Social dominance among members of resident packs can influence access to clumped food resources, such as ungulate carcasses (Gese et al. 1996a, 1996b). Older, experienced pack members are also more successful hunters of both large prey (Gese and Grothe 1995) and small mammals (Gese et al. 1996c). In addition, dominant individuals with access to carcasses are less likely to disperse (Gese et al. 1996a). Consequently, dominance and territoriality play an important role in regulating coyote numbers. The acquisition of a territory is important because territorial individuals are more apt to survive, have more breeding opportunities, and are more likely to have access to carcasses in winter than transient individuals (Andelt 1985, Bekoff and Wells 1986, Gese et al. 1989, 1996a, 1996b). Non-breeding individuals of a pack could be considered surplus, but comprise a significant portion of populations (Gese et al. 1996a).

Effects of Exploitation on Demographics of Coyote Populations

There have been few detailed studies of unexploited coyote populations (populations in which people do not remove animals) and demographic parameters are frequently omitted, but compared to exploited populations, some demographic differences are emerging (Andelt 1985, Crabtree 1988, Gese et al. 1989, 1996a, Windberg 1995, Windberg et al. 1997a). Unexploited coyote populations typically have older age structures (Fig. 4), high adult survival rates, low reproductive rates (especially among yearlings), and low recruitment into the adult population (Andelt 1985, Windberg et al. 1985, Crabtree 1988, Gese et al. 1989, 1996a, 1996b, Windberg 1995). Such populations may have larger packs or social units depending on available food. Under heavy exploitation, populations are characterized by younger age structures, lower adult survival rates, increased percentages of yearlings reproducing, increased litter size, and relatively small packs (Gier 1968, Knowlton 1972, Berg and Chesness 1978, Davison 1980, Andelt 1987). Although litter sizes may increase in response to reduced coyote density (compensatory reproduction), this is likely a response to reduced competition for food (Andelt 1987, 1996) or breeding among younger females. Mean litter size in an unexploited coyote population in Yellowstone National Park increased over 3 years in response to increased availability of ungulate carcasses during winter (Gese et al. 1996a, 1996b).

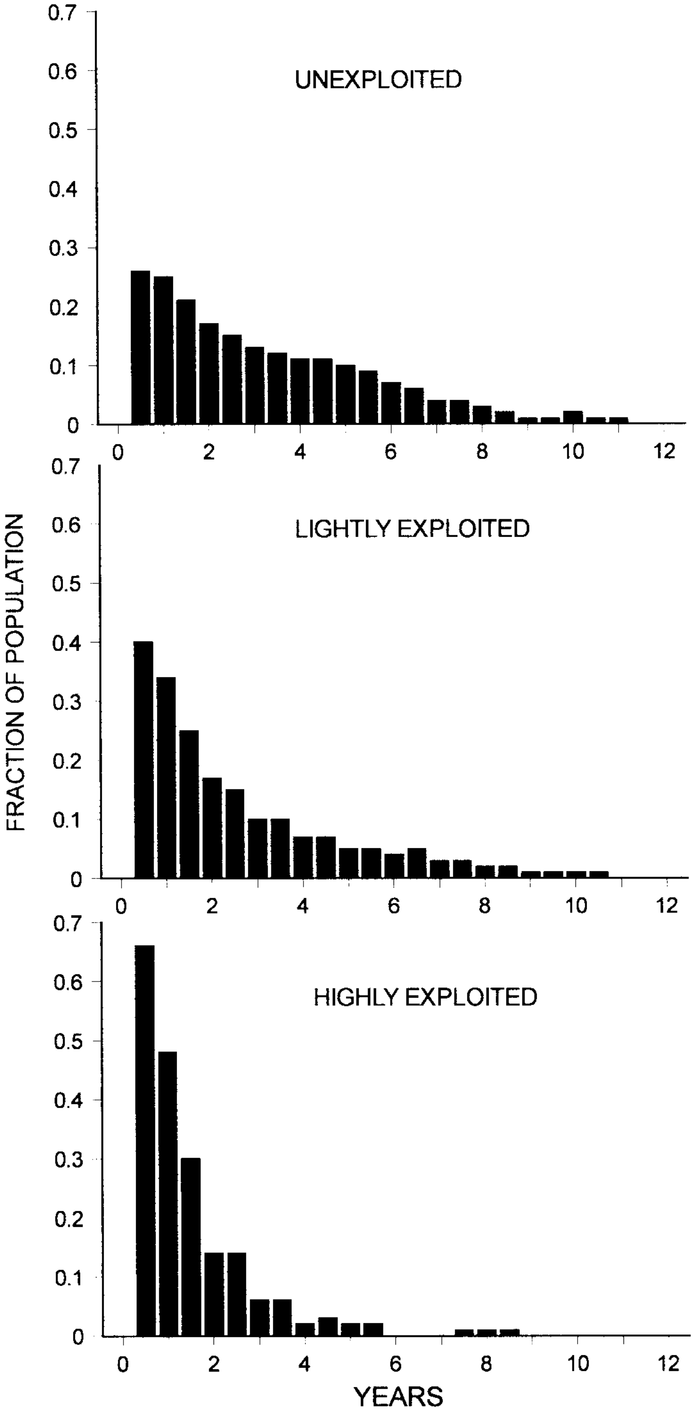

Fig. 4. One-year running means of the age structures of unexploited (n=4), lightly to moderately exploited (n=7), and highly exploited (n=3) coyote populations. Data from Knowlton (1972), Knudsen (1976), Davison (1980), Tzilkowski (1980), Crabtree (1988), and Gese (unpubl. data).

Seasonal Fluctuations in Coyote Abundance

Coyotes are territorial year-round, living in summer where they can survive in winter (Weaver 1979, Gantz 1990, Shivik et al. 1996). Hence territory density remains relatively constant, basically changing only with long-term changes in food base. On the other hand, the size and structure of coyote packs, and hence populations, change seasonally. Births, deaths, and dispersal all have seasonal patterns (Knowlton 1972, Bekoff and Wells 1986, Gese et al. 1996a). The density of coyote populations changes with a pulse, or increase in density, during the whelping season as litters are born, followed by a gradual decline as pups die or disperse and associate pack members leave during winter (Knowlton 1972, Davison 1980, Gese et al. 1996a). When food resources are favorable, pack sizes may remain high over winter (Gese et al. 1996a, 1996b), but only within the limitations established by the available food. Territory density typically remains relatively stable, changing only with long-term changes in the prey base. Concurrently, seasonal patterns in births, deaths, and movements, as mediated by available food, affect the size of coyote packs, and hence coyote density.

Coyote Depredations on Livestock

The amount of damage producers attribute to coyotes can be a volatile and contentious issue. Some people claim few or no depredations actually occur and accuse producers of grossly exaggerating loss estimates. In contrast, producers indicate losses caused by coyotes can be serious and threaten the economic viability of their enterprises. There have been a series of reviews documenting the economic importance of livestock depredations (Caine et al. 1972, Balser 1974, Gee et al. 1977, U.S. Fish and Wildlife Service 1978). Wagner (1988) provided one of the more comprehensive reviews of the topic.

The economic value of livestock lost to predators has been reported as $19–38 million to sheep producers in 1977 (U.S. Fish and Wildlife Service 1978), $75–150 million among lambs, ewes, and calves in 1980 (Wade 1982) and $83 million for sheep and lambs in 1987 (Terrell 1988). More recently, Connolly (1992) compared predation loss estimates for sheep and goats among 3 reports (Pearson 1986, General Accounting Office 1990, U.S. Department of Agriculture 1991) and assessed reasons for the vastly different estimates in losses reported and the economic values involved. In part, variability was attributed to differences in the scope of the studies, different assumptions regarding stock inventories, inclusion or exclusion of pre-docking losses of lambs, use of different assumptions and procedures in compiling the loss data, and different monetary values assigned to animals lost. These 3 studies dealt only with direct losses and did not include indirect costs incurred by the livestock industry, or consumers, associated with predation, including costs of intensified husbandry practices, stock replacements, depredation control efforts, contributions to control agencies, and increased prices resulting from reduced supplies (Connolly 1992).

The varied nature of the sheep and goat industries, including size of individual enterprises, differing intensities of husbandry, and various environmental circumstances within which producers operate, makes any simplistic assessment of losses and loss patterns misleading. The number of sheep in the U.S. has declined over 75% in the past 50 years (Wagner 1988). By 1991, the number of sheep in the U.S. was estimated at 11.17 million, with numbers declining to 8.46 million by 1996 (U.S. Department of Agriculture 1997). In 1974, 35% of the producers had fewer than 25 ewes each and accounted for only 2% of the sheep in the west (U.S. Fish and Wildlife Service 1978). At the same time, 6% of the producers had more than 1,000 ewes each, and accounted for over 55% of the sheep. This variability among producers poses important problems in portraying loss patterns, because there is little information regarding the degree to which individual producers stay within the same portion of the loss spectrum from year to year. Depicting losses based upon accumulated experiences of individual producers exaggerates the importance of smaller producers and minimizes the role of larger producers with the preponderance of sheep. In contrast, basing losses on numbers of sheep may reasonably depict the overall impact of predators upon the sheep population, but may distort the impact on individual producers, especially the smaller ones.

Generalizations about the Magnitude of Losses

Three major types of studies have been used to assess the magnitude of coyote predation upon sheep: (1) studies where research personnel monitored flocks to account for missing sheep and lambs, (2) producer interviews, and (3) questionnaires mailed to producers or telephone surveys soliciting responses. Advantages and biases associated with each type of study are discussed by Wagner (1988). Field studies should provide the best estimate of losses but do not account for, nor identify, all causes of loss. They are costly in terms of time and resources, and thus have only been used in the context of a few research studies. Interviews with producers are also labor intensive, but larger samples can be accrued. Data obtained, however, are subject to the degree to which producers locate missing animals and accurately identify and report causal agents. Mailed questionnaires or telephone interviews provide the largest amount of information for the time and effort expended but are subject to the same biases as interview responses, with additional biases associated with non-responders. As a result, predation loss estimates vary considerably, as does the degree to which the results can be generalized among sheep areas of the country.

In biologically monitored situations where there were organized depredation control efforts, losses of sheep to coyotes typically range between 1.0–6.0% for lambs and 0.1–2.0% for ewes (U.S. Fish and Wildlife 1978). In situations where producers were reimbursed for their losses in lieu of predator control efforts (e.g., Henne 1975, 1977, Brawley 1977, Munoz 1977, McAdoo and Klebenow 1978, Delorenzo and Howard 1976, O'Gara et al. 1983), losses to coyotes were typically higher, ranging from 12–29% of lambs and 1–8% of ewes. Data from various questionnaire surveys suggest lower average loss percentages, ranging from 1–5% for lambs and 0.1–2.5% for ewes (U.S. Fish and Wildlife Service 1978), but neither the type nor intensity of control measures was identified. The latter samples a wider portion of the sheep industry and, therefore, may be a better overall estimate, but also represents inclusion of many small producers with more intensive management programs and relatively lower losses.

While the foregoing provides an overview of losses of sheep and lambs to coyotes, losses were typically not distributed equally among sheep producers. Balser (1974) and Gee et al. (1977) indicate about half of producers report <5% loss of sheep to coyotes, a quarter report 5–10% loss, one in 10 report losses of 10–15%, and the remainder report losses >15% of their flocks. Because the consistency with which individual sheep management units recur within the same portion of the loss spectrum has not been studied, it currently is not practical to use these extensive data sets to assess the degree to which environmental conditions, husbandry practices, and predator management programs contribute to the loss patterns. Also, differences in loss rates could be attributable, in part, to the efforts that producers make in accurately assessing the mortality agent (i.e., confirmation of a coyote kill via necropsy).

Factors Influencing Depredation Rates upon Sheep

Various factors influence coyote depredation rates on sheep, including: breed of sheep, sheep management practices, coyote behavior, environmental factors, and depredation management programs. Sheep have been selectively bred for thousands of years to produce animals that are tractable and suited to particular husbandry techniques, geographic regions, environmental conditions, and cultural requirements, as well as providing desirable characteristics in food and fiber. Changes in animal size and behavior patterns occurred coincident with other developments. Differences in group cohesiveness, sociality, grazing dispersion, attentiveness, and maternal protection may affect vulnerability among breeds. Potentially, husbandry practices may be more important. Confinement, use of predator fences, and shed lambing are practices that can reduce losses. Any reduction in losses, however, is generally achieved at a cost, with many techniques more amenable to small operations than large. Shed lambing is practiced by some large operators with increased lamb survival offset by higher investments in facilities and labor and is used primarily where supplemental feeds are available. Frequently this practice defers predation for 2–3 weeks until the animals return to open pastures and ranges. There may also be a difference in predation risk between pastured versus roving bands of sheep on the range. Theoretically, roving bands of sheep would be exposed to multiple territories of coyotes that may kill sheep, thus increasing predation risk, while pastured sheep would only be exposed to the resident coyotes occupying territories which overlap the sheep pasture (Sacks 1996).

Gluesing et al. (1980) examined behavioral characteristics of sheep to identify characteristics that might be associated with animals within a flock that were most apt to be killed by coyotes. Lambs with impaired mobility, lambs of ewes with impaired mobility, lambs without ewes, lambs displaying aberrant behavior, and lambs that were more active than others were more likely to be killed. Lambs newly introduced to a flock were more likely to be killed than lambs well-integrated into the social structure of flocks; a finding supported by Blakesley and McGrew (1984). It appears that factors which tend to place lambs on the periphery of flocks increase their chances of being killed. Scrivner et al. (1985) indicated that lambs from multiple births had a higher probability of being lost than lambs of single births, although they were unable to specifically assign predation as the cause of loss.

Two aspects of coyote biology warrant consideration: coyote abundance and coyote behavior and learning. Are depredations directly related to coyote abundance? The literature provides information on both sides of the issue. Sheep losses in an area in south-central Idaho were closely related to coyote density, which fluctuated in synchrony with jackrabbit abundance (Stoddart, unpubl. data). In contrast, small sheep flocks in south Texas survive in the midst of some of the highest coyote densities known (Knowlton and Gese 1995). Behavioral differences among coyotes may influence their likelihood to kill. This suggests not all coyotes kill sheep, or that individuals will kill sometimes and not at other times. Many coyotes are never exposed to sheep (Wagner 1988). In some cases, coyotes do not develop sheep-killing behaviors, even when coerced under pen conditions (U.S. Fish and Wildlife Service 1978, Timm and Connolly 1980). Several studies in California (Conner 1995, Shivik 1995, Sacks 1996, Shivik et al. 1996) report numerous radio-collared coyotes in the vicinity of sheep with few, if any, recorded losses of lambs. In these studies, most confirmed coyote kills were directly attributable to predation by breeding, territorial coyotes while other coyotes appeared to be innocuous with regard to depredations. In another study, 6 of 11 coyotes removed by aerially gunning on 4 ranches in Montana showed evidence of having depredated sheep (Connolly and O'Gara 1987, Connolly 1988). Similarly, in an unexploited coyote population, Windberg et al. (1997b) noted 65% of the coyotes exposed to a herd of goats fed upon them even though the goats were present for only 21 days. It is not known how many of these coyotes were involved in actually killing the goats, but >40% of the kids in the herd were killed.

The roles of motivation and learning in coyote depredations have not received adequate attention. Coyotes feed principally on small and medium-sized prey, such as rodents and rabbits, but they do learn to kill and feed on larger prey. Till and Knowlton (1983) demonstrated that provisioning young is an important motivation for territorial coyotes to switch to killing lambs. Interestingly, this behavior is reversible because when the coyote pups were removed, the adults responsible for the depredations usually stopped killing sheep. In contrast, territorial coyotes at the Hopland Field Station, Calif., frequently start killing lambs soon after they become available in December and January, well outside the normal pup-rearing season (Conner 1995, Sacks 1996). Evidence is accumulating among several canid species suggesting the alpha pair of territorial social groups, especially the males, are the principal actors when killing large prey (Peterson 1977, Mech 1988, Gese and Grothe 1995, Sacks 1996). Understanding these parameters has important implications for the development of more benign and selective depredation control techniques and programs.

Affect of Prey Abundance upon Depredation Rates—Coyote diets, and their associated predation patterns, shift when abundance of one or more prey species change (Hoffman 1979, Hamlin et al. 1984). Some authors (McAdoo 1975, Guthery 1977, Kauffeld 1977, Gober 1979) have found these concepts also apply, to some degree, to coyote predation on sheep (i.e., coyote predation rates on sheep are inversely related to abundance of natural prey). Most of these studies involved seasonal or short-term shifts in prey abundance and did not consider the potential numerical response of coyote populations as a result of long-term changes in prey abundance. Long-term availability of prey is one determinant of coyote density (Clark 1972, Knowlton and Stoddart 1983, Knowlton and Gese 1995), and there is evidence of a positive association between coyote density and predation losses of sheep (Wagner 1988). A 6-year study in Idaho (Stoddart, unpubl.

data) found predation rates on sheep increased in direct proportion to changes in coyote abundance, which responded to changes in the abundance of jackrabbits. The increase in coyote density was believed to be due to increased pack size. Whether the alpha pair increased predation on sheep in response to increased pack size (i.e., increased competition), or associate pack members also killed sheep and thus increased overall depredation rates, is unknown. In addition, there was a temporary, but dramatic escalation of depredation on sheep when the hare population collapsed and coyotes had no alternative food source.

Other Considerations—Only recently have food-caching behaviors among coyotes been recognized and documented, although they now appear to be quite common (Weaver 1977, Windberg et al. 1997b). Caching typically occurs when more food becomes available than a coyote, or group of coyotes, can consume at a given time. The degree to which food-caching is a factor in the failure to locate missing livestock (e.g., Scrivner et al. 1985), especially small lambs and kids, is not known but caches of complete jackrabbits, and heads, shoulders, and hind quarters of 15–20 pound lambs and kid goats are well documented (Stoddart, unpubl. data; Windberg et al. 1997b).

There is speculation (e.g., Wilkinson 1996) that coyote populations not subject to human-induced mortality might pose less risk to livestock than populations manipulated to reduce coyote abundance. The underlying rationale suggests undisturbed coyote populations have fewer and smaller litters, resulting in reduced motivations to feed pups, and translate into reduced depredations on livestock. While there is evidence suggesting litter sizes might change (Crabtree 1988, Knowlton and Gese 1995, Windberg 1995, Windberg et al. 1997a), evidence that fewer litters would be produced is meager; simultaneous measures of both reproductive rates and population size from populations in similar environments would be needed to clarify this issue. To date, this has not been done. Low productivity among unexploited coyote populations has been reported (Knowlton 1972, Crabtree 1988, Gese et al. 1989, Windberg et al. 1997a). In contrast, Windberg et al. (1997b) reported 41% of 34 kid goats were killed by coyotes within 3 weeks of the time they were released within an unexploited coyote population with very low reproductive rates (Windberg et al. 1997a). Although which coyotes killed goats was not determined, both territorial and transient, as well as males and females fed on the goats. In addition, Sacks (1996) and Conner (1995) reported extensive predation on lambs in California during December and January when coyote pups were not present, indicating that provisioning pups is not the only motivation for coyote predation on lambs.

Depredation Control

Protecting livestock from coyote depredations is a complex endeavor, with each case frequently requiring a unique assessment of the legal, social, economic, biological, and technical aspects. The general philosophic approach outlined by Slate et al. (1992) for formulating procedures to resolve individual problems is well-recognized. Successful resolution of wildlife conflicts involves the anticipated efficacy, selectivity, and efficiency of various management approaches, including both corrective and preventive techniques. Perennial patterns of depredations are also involved. Programs and procedures that are more benign in their affects on wildlife, including coyotes, should be preferred to those creating greater perturbations.

The variety of motivations, circumstances, and conditions in which predation occurs precludes the likelihood any one procedure will effectively prevent or resolve most depredation problems. Consequently, a variety of tools and applications have been developed to fit different situations. Fall (1990) and Andelt (1996) identified many of the techniques available for reducing coyote depredations, from deterring problems to removing individual animals or populations posing risks to other human endeavors. The intent here is to examine data regarding the efficacy of various techniques and factors that appear to affect their usefulness.

Non-Removal Techniques

A diverse array of procedures have been used to create physical barriers between coyotes and livestock or to deter coyotes from attacking livestock (Linhart 1984a, Wagner 1988, Fall 1990, Green et al. 1994). Most non-removal depredation control procedures fall within the operational purview of livestock producers. While there are reports of success with many such methods, failures are common, few have been subjected to experimental tests, and none have proven universally successful. Additional information is needed to clarify the factors that influence the success of individual techniques.

Livestock Husbandry Practices—Although various livestock management practices have been repeatedly suggested as means of reducing depredation losses (Robel et al. 1981, Wagner 1988), few have been systematically scrutinized under controlled conditions to determine their efficacy, costs, and benefits. Some of the more frequently mentioned practices include: (1) confining or concentrating flocks during periods of vulnerability (e.g. at night or during lambing), (2) using herders, (3) shed lambing, (4) removing livestock carrion from pastures to retard food recognition by coyotes, (5) synchronizing birthing to reduce the period of maximum vulnerability, and (6) keeping young animals in areas with little cover and in close proximity to human activity. These procedures generally require additional resources and efforts, and frequently only delay the onset of predation, or have undesirable side effects. For example, penning animals at night requires additional effort and frequently creates spot deterioration of pastures and ranges. Similarly, shed lambing decreases the mortality of lambs from many causes but requires additional labor as well as a ready and affordable supply of feed. For these procedures to be effective, producers must develop specific strategies tailored to their own situations, recognizing that definitive economic advantages may be difficult to demonstrate.

Fencing—Various configurations of fencing can exclude or deter coyote use of specific areas (de Calesta and Cropsey 1978, Linhart et al. 1982, Shelton 1984, 1987, Nass and Theade 1988), but few can be identified as being "coyote-proof" because coyotes learn to dig under or jump over fences. Installation costs usually preclude the use of effective fences except where high value commodities are concentrated in small areas. The dispersed nature and low economic density associated with most sheep grazing in the semi-arid regions of the western United States makes fencing an impractical procedure for preventing depredations. In addition, fencing that denies access to coyotes will likely inhibit movements of other wildlife species.

Frightening Devices—Electronic devices that periodically emit bursts of light or sound have been shown to deter coyote predation on sheep in both fenced pastures (Linhart et al. 1982, Linhart 1984b, Linhart et al. 1984) and on open range situations (Linhart et al. 1992). Other studies (Bomford and O'Brien 1990, Koehler et al. 1990) report benefits from such devices are variable and short-lived. Linhart et al. (1992) argued that habituation by coyotes can be retarded if the devices are used in appropriate numbers, moved periodically, and programmed to vary the temporal pattern of multiple stimuli. Use of such frightening devices are not widespread, partially because use of sirens and strobe lights at night near people is not acceptable.

Guard Animals—Use of guard animals appears to be a promising way of encouraging coyotes to avoid livestock. Dogs, llamas, and donkeys or mules are most commonly mentioned as livestock guards. The most extensive evaluations have been with dogs (Linhart et al. 1979, Coppinger et al. 1983, Black and Green 1984, Green et al. 1984, Green and Woodruff 1983, 1987). While dogs appear effective in some situations (e.g. Linhart et al. 1979), they are not in others (Timm and Schmidt 1989, Conner 1995). Reasons for this are not fully understood, but sheep can be very difficult to protect when they are in large flocks, dispersed over rough terrain, and where there is thick cover for coyotes. In addition, training and close supervision of the dogs seem important to success. Some poorly trained or supervised guard dogs have killed sheep and lambs, harassed or killed wild animals, and threatened people that intruded into the dogs' domains (Timm and Schmidt 1989). In instances where guard dogs are ineffective, their presence frequently precludes that use of other techniques (e.g., traps, snares, M-44's) or reduces the efficiency of others (e.g., calling and shooting).

Llamas may be more practical for many situations (Powell 1993). They can be kept in fenced pastures, do not require special feeding programs, are usually tractable, and have a relatively long working life compared with dogs. Evaluations currently in progress are promising (Cavalcanti 1997, Meadows 1999) but further study of the circumstances in which llamas are effective is needed and the degree to which coyotes may habituate to their presence needs to be assessed. To date, there have been no systematic field studies of the behavior of coyotes toward guard animals. Radioed coyotes have been found in close proximity to sheep bedding grounds and the attending guard dog (Conner 1995). One hypothesis is that although guard animals may not deter coyotes from grazing areas, they may change the coyotes' agenda when in those areas.

Repellents and Learned Aversions—At present, there are no commercially available repellents that effectively deter coyote predation. A variety of noxious gustatory, olfactory, and irritating products have been tested in captive situations. A few show promise for reducing food consumption. These include pulegone, cinnamaldehyde, and allyl sulfide (Hoover 1996). While repellents, including quinine hydrochloride and capsaicin show promise in discouraging coyote damage to inanimate items like irrigation hoses (Werner et al. 1997), there is meager information demonstrating these substances deter predation (Lehner 1987). Available evidence suggests attacks continue despite presence of these materials, although different sites of attack are sometimes employed (Burns and Mason 1997).

Conditioned taste aversion, using lithium chloride, to reduce coyote depredations on sheep received much scientific attention in the 1970's and 1980's. Results of studies have been equivocal, with some investigators reporting success (Gustavson et al. 1974, Ellins and Martin 1981, Gustavson et al. 1982, Forthman-Quick et al. 1985a, 1985b), while others were either unable to replicate those research findings or to make them effective in field situations (Conover et al. 1977, Burns 1980, Bourne and Dorrance 1982, Burns 1983, Burns and Connolly 1985). In pen tests, coyotes frequently distinguished between treated and untreated baits, avoided the former, and did not generalize aversion of baits to live prey (Burns and Connolly 1980). While lithium chloride reduces consumption, it does not deter predation. There are indications that positive reinforcement from prior predatory acts may interfere with acquisition of associations between sheep ingestion and sickness (Conover et al. 1977, Burns 1980). Ten years after the most extensive field trials involving use of lithium chloride (Gustavson et al. 1982, Jelinski et al. 1983), a survey of the same sheep producers revealed that while 54% of the original participants considered the technique "successful" or "somewhat successful," only one still used it (Conover and Kessler 1994). In addition, only 3 of 47 randomly selected producers in that region had ever used the technique and only one used it the year prior to the survey (Conover and Kessler 1994). Available evidence suggests conditioned taste aversions, as attempted to date, are either ineffective or unreliable methods of depredation control.

Reproductive Interference—Initial attempts to influence the reproductive process of coyotes with chemical sterilants assumed reduced reproduction would reduce coyote population levels and that fewer coyotes would result in fewer depredations (Balser 1964). This procedure was appealing because it attempted to resolve depredations without killing coyotes. Trials with diethylstilbesterol indicated reproduction could be thwarted (Balser 1964, Linhart et al. 1968), but timing was critical and the approach was impractical without effective bait delivery systems (see Kirkpatrick and Turner 1991 for a review). In the mid-1970s, registration of any material with potentially broad spectrum effects in field applications appeared unlikely and research development on this substance was curtailed. Currently there is renewed interest in reproductive inhibition using immunocontraception (Miller 1995, DeLiberto et al. 1998). Although such techniques are presently unavailable for coyotes, it is anticipated that species specific materials with reversible effects may become available.

An alternate paradigm for interfering with reproductive processes involves sterilizing territorial, breeding coyotes in vicinities where chronic depredations occur. This strategy is predicated on research indicating depredations can be reduced by removing pups of depredating coyotes (Till and Knowlton 1983) and assumes: (1) territorial breeders are the principal killers of livestock; (2) they will continue to maintain territories while sterile; and (3) depredations in some areas are linked to the presence of pups. The first assumption is supported by Sacks (1996); and the second appears likely on the basis of pen studies (Zemlicka 1995). However, research in north-coastal California, where depredations peak during a lambing season which is out-of-phase with pup-rearing (Scrivner et al. 1985, Conner 1995, Sacks 1996),suggests that presence of lambs, rather than pups, may also be an important determinant of predation patterns.

Although coyote predation can be deferred by non-removal techniques, coyotes frequently habituate, or adapt, to the presence or use of such procedures. This probably happens more quickly when alternative foods are limited or when energy demands are high (e.g., during pup rearing). In some instances, procedures which rely on fright or avoidance appear adequate, at least on a temporary basis. In others, coyotes continue to investigate, and kill livestock in the presence of non-removal depredation control techniques. For example, Conner (1995) documented coyotes killing sheep in close proximity to a radiocollared guard dog.

Coyote Removal Techniques

When depredations can not be stopped effectively and efficiently with non-removal techniques, removing one or more coyotes may be needed to temporarily reduce risks to livestock. In some instances, removal of 1 or 2 individuals may suffice, and in others, coyote population reduction may be warranted. Factors affecting selection of the specific option(s) include: (1) nature of the problem; (2) presence or absence of historical patterns; (3) relative size of the area involved; (4) season of the year and timing with regard to depredations or anticipated depredations; and (5) the efficacy, selectivity, and efficiency of specific removal methods or procedures. While most non-removal depredation control techniques fall within the purview of livestock producers, most procedures and techniques that rely on coyote removal are relegated to programs administered by wildlife management agencies due to: (1) the sophistication and technical expertise required; (2) regulatory and accountability concerns; and (3) the need for coordination.

Techniques for Removing Offending Coyotes—Removing individual coyotes responsible for depredations is especially suited to small areas where specific coyotes pose immediate risks. Resolution at this scale is generally corrective in nature (i.e., stopping ongoing depredations) and typically requires the highest levels of skill in depredation control. Calling and shooting, with or without the help of lure dogs, can be a selective means of removing coyotes that kill livestock, particularly during denning and pup-rearing seasons (Alcorn 1946, Coolahan 1990). This procedure is extremely selective for coyotes, with selectivity for individuals responsible for depredations dependent on the accuracy of identifying areas used by them.

Where livestock can be effectively manipulated, Livestock Protection Collars can selectively remove specific coyotes responsible for depredations (Burns et al. 1988, 1996, Connolly and Burns 1990, Connolly 1993, Rollins 1995). These devices are registered by the Environmental Protection Agency (EPA) for use by ranchers in states with approved training and accountability programs. Currently, 7 states have EPA-approved programs, with approvals pending in others. The collars have toxicant-containing pouches that are punctured when coyotes attack the sheep's throat, thereby releasing the poison into the coyote's mouth. This may be the most selective procedure for removing specific coyotes responsible for killing livestock, but it is not always efficient because of the inherent difficulty in anticipating which sheep or lambs are most likely to be killed.

Coyotes causing depredations can be removed with traps, snares, and M-44 devices, but the efficiency of capture and selectivity for coyotes in general, and offending individuals in particular, is usually lower. Most depredations can be attributed to territorial, dominant coyotes (Till and Knowlton 1983, Sacks 1996), with depredations usually occurring within the territorial boundaries of the animal(s) responsible (Blejwas, unpubl. data). Unfortunately, coyotes are less vulnerable to capture devices when encountered within familiar areas (Harris 1983, Windberg and Knowlton 1990, Windberg 1996), making removal of offending individuals difficult (Conner 1995, Sacks 1996) and the risk of capturing coyotes from surrounding areas greater (Hibler 1977, Windberg and Knowlton 1990). In addition, persistent exposure to capture devices can reduce their effectiveness (Andelt et al. 1985, Brand et al. 1995).

Coyote Population Reduction Programs—There are a variety of situations where reducing the number of coyotes is desired, including situations where coyotes pose a risk to other wildlife species (Guthery and Beasom 1977, Connolly 1978, Smith et al. 1986, Teer et al. 1991, Cypher and Scrivner 1992, Henke 1995), when spread of infectious diseases need to be curtailed (Clark et al. 1994, Clark and Wilson 1995), and when more benign depredation control techniques are ineffective. Meeting such objectives usually involves removing significant portions of the coyote population. However, which coyotes and how many coyotes to be removed, are recurring problems with non-selective removal programs. The resilience of coyote populations dictates that the size of the area involved (Stoddart et al. 1989), the intensity and persistence of effort, timing of removal with respect to vulnerability of prey, as well as normal demographic processes of coyotes, must be considered. Effecting removals as close as practical to the anticipated risks, both in time (Knowlton 1972) and proximity (Stoddart et al. 1989), is important. Even under the most severe removal programs, repopulation by coyotes can be expected within months (Beasom 1974) or 2–3 years (Connolly and Longhurst 1975, Connolly 1978, 1995). Repopulation is particularly fast on small areas, such as individual ranches or pastured sheep operations. Effects of population reduction programs are most persistent when efforts are conducted over large areas (Stoddart et al. 1989) and occur after the dominance and territorial patterns of coyotes are set for the coming breeding period and immediately prior to whelping. This timing reduces the possibility of other coyotes repopulating the area, establishing pair-bonds, and producing offspring within the current breeding season (Knowlton 1972, Connolly 1978, 1995). One of the more effective programs of population reduction occurred on the Edwards Plateau of Texas where coyotes were almost eradicated between the 1920's and 1950's (Nunley 1995). That effort was aided by a pervasive distribution of sheep and goats in the area, extensive use of netwire fencing that helped identify coyote travel patterns, and population reduction programs around the perimeter that reduced immigration. Deteriorating netwire fences, fractionation of the grazing areas (and hence the coyote reduction program), and reduced coyote control efforts around the periphery of the Plateau likely contributed to a resurgence of coyotes since 1970 (Pearson and Caroline 1981, Nunley 1995).

Depredation management in the form of preventive control (Wagner 1988) is a preemptive removal of coyotes from areas with historic patterns of depredations, frequently where other types of depredation control are not feasible or effective, or where coyote depredations are a perennial and chronic problem. It is predicated partially upon the assumption that livestock losses are directly related to the numbers of coyotes present, and that removal of coyotes will produce a proportionate reduction in depredations. This is consistent with the observation of a positive linear relationship between coyote abundance and sheep depredations (Stoddart, unpubl. data). Another study indicated that over a 7-year period the depredation rate on sheep on the Honn Ranch, Wash., was inversely related to the number of coyotes removed (Stream 1976). In contrast, examination of a 12-year data set from a California sheep ranch (Conner et al. 1998) found that killing remained high in some years despite corrective removal of coyotes and there was no correlation between the numbers of coyotes removed and the numbers of sheep subsequently killed. Thus, a fundamental question remains: does partial, nonselective removal of coyotes effectively reduce depredations on sheep? Since removal of all coyotes from an area will, temporarily, eliminate coyote predation, the question really relates to the theoretical nature of the relationship between coyote removal and depredation rates. Assumptions about the duration of the effect are also involved.

Preventive depredation control efforts on mountain pastures, particularly winter removal of coyotes from summer grazing allotments, has been criticized because of the 5–6 month lapse between coyote removal and anticipated losses during the ensuing summer grazing season. Examining coyote movements in montane areas, Gantz (1990) found that territorial coyotes used the same areas in winter as they do in summer; a finding similar to that of Weaver (1979) and Shivik et al. (1996). Hence, animals removed in winter would likely include animals living and rearing pups in those areas the following summer. Wagner (1997) evaluated aerial hunting on mountain grazing allotments where coyotes were removed in January and February, when coyotes were more vulnerable due to environmental conditions (snow cover), and documented the subsequent sheep losses during summer following winter aerial hunting. On allotments receiving aerial hunting (treated), lamb losses to all causes declined 25%, while lamb losses to all causes declined 6% on untreated allotments. The number of lambs confirmed to be killed by coyotes declined by 7% on treated allotments, whereas lambs killed by coyotes increased 35% on allotments receiving no aerial hunting. Confounding variables in this study were the relatively high sheep losses on the control and treatment areas, as well as the degree of coyote removal on all the grazing allotments prior to the study.

Demographic Consequences of Coyote Population Reduction—Because coyote populations are dynamic and resilient, effects of coyote removal are ephemeral, with normal demographic responses attempting to return the population to levels consistent with available food and habitat conditions. These responses include: recolonization from adjacent areas, increased breeding among younger females, increased litter size, and increased survival rates. The speed with which populations return to “normal" levels is dependent upon the size of area involved and the intensity of the removal program. On small management units, immigration of non-territorial coyotes from surrounding areas should occur rapidly, probably within weeks or months. On larger areas, recruitment would come from immigration as well as increased productivity by surviving coyotes. A temporary increase in juvenile survival could also be expected. Although we would expect higher reproductive rates, speculations that more pups might be recruited into a reduced population, and thus increase population density beyond the preremoval level, are unwarranted because competing rates of change are involved (i.e., any increased reproductive rate would be applied to a smaller population). At this point, the relationship between the degree of reduction and increased productivity remains conjectural. Similarly, increased survival of coyote pups could be expected, but expectations that population levels would exceed those dictated by available food resources are unrealistic.

The effectiveness of coyote population reduction on small management units (Stoddart et al. 1989) or with inadequate intensities of effort are apt to be disappointing (Beasom 1974). Including a buffer zone around the primary reduction area (Stoddart et al. 1989) could enhance the effectiveness of removal programs because it would provide vacant territories to absorb some dispersing coyotes that might otherwise infiltrate the primary protection zone (Knowlton 1972, Davison 1980). However, establishing a buffer zone removes territorial animals from adjacent areas that are probably “staying home" and not involved in the localized depredation problem (Sacks 1996). Establishing a buffer around protection zones may be neither socially or politically acceptable as well. Depredation relief resulting from a coyote population reduction program should be considered transitory, unless the removal program is maintained. Decisions about the timing and intensity of such efforts should incorporate information about the period that protection is needed, when populations are vulnerable, as well as the phenologies associated with coyote biology.

Synthesis

Some coyotes kill domestic stock and persistent depredations can place some livestock producers in economic jeopardy. Various techniques can prevent or curtail predation on livestock but none are universally effective. Most techniques used to prevent coyote depredations do not involve removing coyotes and typically involve activities relegated primarily to livestock producers, while removing coyotes to solve depredation problems is typically more effectively done by wildlife management personnel.

Unfortunately, the dominant territorial animals most likely to cause depredations are also more difficult to remove. Differences among depredations, the circumstances in which they occur, and the behaviors and motivations among coyotes makes simple resolution of problems unlikely.

Typically, nonlethal techniques are initially attempted by livestock producers when they experience depredations by coyotes. Some success can be achieved with the use of fencing on small pastures, improved husbandry practices (e.g., shed lambing, having shepherds present) on small and large operations if economically feasible, or guard animals on larger fenced operations where open habitat allows guard animals to detect coyotes. Guard dogs frequently limit the use of other techniques (e.g., trapping, calling and shooting) because techniques used to attract coyotes also attract guard dogs. Llamas appear effective, particularly when placed singly with stock (i.e., 2 llamas may ignore the sheep) and in open habitat allowing them good visibility and less concealment for coyotes. These approaches can be implemented with some success, but require additional labor and expense to the producer. Although they may be initially effective, frightening devices become ineffective as coyotes habituate to them. At present, aversive conditioning appears to be a nonviable option because, while it stops the consumption of food, it apparently fails to prevent predatory motivations. Currently, there are no effective repellents that deter coyote predation, only consumption or avoidance of inanimate objects. Presently, reproductive intervention to modify the predatory behavior of coyotes holds promise as a technique and warrants continued investigation. This technique may work well in the intermountain west where sheep are a seasonal and temporary food source for coyotes. However, in areas where sheep are perpetually present (e.g., coastal California, Texas), sheep become part of the prey base and are a year-round food source, with coyote predation not tied to pup production. With regards to the coyotes themselves, it must be remembered that the stimuli for coyotes to chase and kill prey is a strong, powerful, and innate predatory behavior. Nonlethal methods and ideas as to how to modify this instinctive behavior requires careful thought and innovative research.

Lethal removal usually is implemented when nonlethal procedures are impractical or ineffective. Typically, large operations on open ranges resort to lethal control because fencing is impractical and bands are too large to pen at night or for guard animals and shepherds to effectively patrol. Local population reduction can provide temporary relief to sheep operators, but only until the local coyote population compensates for the removals and fills vacant territories. The more focused removals are to the area of depredations, the shorter the duration of the effect. Population reduction as a management option usually requires annual reapplications due to the reproductive capabilities and ease of movement of coyotes (i.e., dispersal of juveniles and presence of transients). A lethal technique that selectively targets offending coyotes killing sheep is the use of Livestock Protection Collars. However, this technique requires state by state authorization (registration) by the EPA and attendant technical training programs. Traditional methods of capture (traps, snares) can potentially remove offending animals, but can be difficult, and remains relatively nonselective. Regulations regarding lethal control and removal of coyotes must be examined prior to implementing such programs; permits may be required for some activities. Four states (Arizona, California, Colorado, and Massachusetts) currently have restrictions on the use of leg-hold traps. Other states (e.g., Arizona, Utah) have specific limits on aerial hunting practices.

Preferred management options should be those that resolve problems efficiently in the least intrusive manner. This requires a careful analysis of each situation; matching biological, legal, social, and economic considerations with an understanding of the merits and limitations of individual techniques.

There is a continued need for research to examine and evaluate the effects of coyote removal and the efficacy of various control techniques in an objective and statistically sound way (i.e., adequate sample sizes and controls). Development of non-lethal methods, as well as lethal methods which target the dominant, territorial coyotes responsible for the depredation problem, are also needed. There is no "magic bullet" technique that can be recommended to solve all depredation problems on livestock. Successful depredation management requires a variety of techniques used in an integrated program. While the controversy surrounding coyote management will remain emotional, political, and subject to debate, the evolution of coyote depredation management is dependent upon sound research and objective data interpretation.

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J. Range Manage.
52:413–419 September 1999

Viewpoint: The role of drought in range management

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Abstract

Drought is an ambiguous term, subject to expectation and the weight of emphasis on meteorological, agricultural, hydrological and socio-economic dimensions. Uncertainty associated with the identification of drought often results in a lagged response in reducing stocking rates. This delay reduces vegetation cover, increasing the potential for accelerated erosion following the drought. The long-term consequences of accelerated erosion are a reduction of soil depth, a decline in soil structure and a decrease in infiltration rate and water storage capacity. Less water stored on a site hastens the onset of plant stress, effectively increasing the perceived frequency and consequences of drought. Management and policy tools must improve the integration of economic and ecological aspects of drought-induced de-stocking decisions, especially by incorporating the long-term irreversible costs of erosion.

Key Words: climate, desertification, erosion, grazing management, hydrologic cycle

Drought is a multi-faceted concept which defies attempts at precise and objective definition. This ambiguity causes confusion and indecision, resulting in either inaction or ad hoc responses which do not fully consider the complex, long-term ecological and socio-economic interactions associated with water shortages (Wilhite and Glantz 1985). The media and politicians tend to blur and distort public perceptions of drought by characterizing the consequences of drought as something exceptional, thereby portraying drought as a temporary, climatic aberration. Consequently, each time a serious drought occurs, millions of words are written about crop failures, land misuse, overpopulation, and rainfall record (Tannehill 1947), but because drought is often handled in the policy arena as an abnormal event, it usually is not taken seriously in planning once expected rainfall patterns resume. Drought is an inevitable part of normal climate fluctuation and should be considered as a recurring, albeit unpredictable, environmental feature which must be included in planning. Muddled views and lagged responses toward drought pose a threat to sustainable management of rangelands.

Resumen

La sequía es un término ambiguo, depende de las condiciones esperadas y del énfasis en las dimensiones metereológicas, agrícolas, hidrológicas y socioeconómicas. La incertidumbre asociada con la identificacion de sequías resulta frecuentemente en una respuesta tardía en la reducción de la carga animal. Este retraso reduce la cubierta vegetal, aumentando el potencial de una erosión acelerada después de la sequía. Las consecuencias a largo plazo de la erosión acelerada son la reducción de la profundidad del suelo, el deterioro dela estructura del suelo, y la reducción de la tasa de infiltración y de la capacidad de almacenamiento de agua. La reducción del volumen de agua almacenada en un sitio acelera el inicio de stress en la planta, incrementando efectivamente la percepci ón sobre la frecuencia y las consecuencias de las sequías. Las pol ticas y estrategias de manejo deben mejorar la integración de los aspectos económicos y ecológicos de la reducción de la carga animal inducida por la sequía, especialmente incorporando los costos irreversibles y a largo plazo de la erosión.

Perspectives on the Definition of Drought

Much of the confusion about drought results from various perspectives of how to define it. The beginning and end of a drought are hard to recognize because drought is a gradual phenomenon. The effects of drought often accumulate slowly as a dry period begins and may linger after expected rainfall patterns have resumed. Most drought definitions are based on 1) meteorological observations, 2) agricultural problems, 3) hydrological conditions and/or 4) socioeconomic considerations (Wilhite and Glantz 1985). Perception of drought, therefore, depends on how the nuances of these 4 perspectives are blended.

Meteorological Drought Perspective

Most interpretations of drought have a meteorological element as part of the definition. This perspective refers to a significant decrease from the climatologically-expected precipitation. Expectations vary with location and are often site specific. For example, a drought in Bali, Indonesia is defined as a period of 6 days without rain while, at the other extreme, a drought in parts of Libya is identified only after 2 years without rain (Hudson and Hazen 1964). The Society of Range Management Glossary (Kothmann 1974) uses a meteorologi-

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Authors wish to thank A.P. Thurow for her comments on the manuscript.
Manuscript accepted 29 Nov. 1998.

cal-based definition of "prolonged dry weather, generally when precipitation is less than three-quarters of the average annual amount." The Palmer Drought Severity Index (PDSI) (Palmer 1965) is probably the best known meteorologic drought definition in the United States. It relates drought severity to the accumulated weighted differences between precipitation and evapotranspiration (ET).

A common criticism of meteorological criteria to define drought centers on the basis for the calculation of "normal" (Glantz and Katz 1977). By international convention, a 30-year precipitation record generally is considered the basis for a calculation of "normal" (Wilhite and Glantz 1985). This practice does not make use of the entire historical precipitation record available for many locations; therefore it may not adequately reflect the long-term climatic record, especially in semi-arid regions prone to large interannual variation.

Use of the term "normal" is also undermined by a common statistical mistake. Often "normal" is calculated as the arithmetic mean. An arithmetic mean (i.e., summing annual precipitation data and than dividing by the number of years) is not a statistically valid technique for representing "normal" when the data do not have a bell-shaped (parametric) distribution. Improper application of the arithmetic mean calculation may result in annual precipitation being below "average" most of the time. Annual precipitation data are usually highly skewed (e.g., many dry years and a few very wet years). The degree of skewness generally increases as the climate becomes drier (Glantz and Katz 1977). This occurs because occasional meteorologic conditions produce unusually heavy rainfall for a few years of the record. For example, an "El Niño" shift in ocean current results in substantial rains in otherwise arid regions in central Chile, northern Mexico and the southwestern US (Rasmusson 1987, Hunt 1991).

When long-term precipitation data are skewed, as they are for many arid and semi-arid rangelands, a statistically appropriate method for expressing "normal" precipitation is to calculate the median (i.e., the mid-point of the data set, where half of the years are wetter and half are drier than the median value) or the mode (i.e., the amount of precipitation most likely to occur). Neither of these measures are particularly sensitive to skewness and their interpretations are explicit.

Due to the unstable nature and complexity of atmospheric dynamics, the theoretical limit of accurate weather prediction does not exceed a few weeks (Skukla 1985). Much attention has been devoted to searching for trends or cycles of long-term climate; discussion of this issue in the popular press ignores the important aspect of rainfall on many rangelands—its extreme variability. Even if trends or cycles do exist, the inherent variability of seasonal forecasts limit their managerial value (Glantz and Katz 1977, Rasmusson 1987).

Agricultural Drought Perspective

Many identify drought in terms of when water deficits limit vegetation production. From an agricultural perspective a drought occurs when low soil moisture causes extreme plant stress and wilt, and lowers grain yield (Carr 1966) or results in less forage production than expected. This definition is more complicated than simple considerations about the amount of precipitation. By definition it integrates the timing and amount of precipitation with plant water demand (as can be influenced by high temperatures and wind) and available soil water (as can be influenced by the infiltration capacity, soil texture, and soil depth). These considerations led Palmer (1968) to develop the Crop Moisture Index (CMI). The CMI modifies the meteorologically-based Palmer drought severity index (PDSI) to better reflect the considerations of agricultural drought by emphasizing the deficit between actual and expected weekly evapotranspiration (ET). This index is available for the U.S. in the Weekly Weather and Crop Bulletin, published jointly by the U.S. Department of Agriculture and the National Weather Service.

There are a variety of species-specific drought indices designed to analyze various aspects of water supply and demand needed for important agronomic species (cf., Meyer et al. 1993). These indices, based on crop models, tend to characterize drought intensity by emphasizing available water in the topsoil required to meet plant water demand. This rationale considers the amount of water in the topsoil as a critical element of drought calculation because of the interaction of water with root growth, nutrient supplies, and microorganism activity which occur in that zone. Drying of the topsoil layer, therefore, is considered an early indicator of yield loss. These types of species-specific indices are rarely calculated for native forage species, but intercepted photosynthetically active radiation (IPAR) data collected by satellites are increasingly being used to identify regional drought on rangeland. Estimates of IPAR can indicate drought severity by contrasting a region's yearly relative difference of photosynthetic capacity (Tucker and Goward 1987).

Hydrologic Drought Perspective

A hydrologic drought is defined as a period when surface and groundwater availability is inadequate to supply established uses (Linsley et al. 1975). Therefore, this definition of drought focuses attention on the drying of streams and rivers, depletion of water stored in surface reservoirs and lakes, lower than normal accumulation of snowpack in the mountains, and decline of ground water levels. This concept of drought is often used by regional planners who are concerned with amenities such as municipal and/or irrigation water supply, hydro-electric power generation, and recreational opportunities. This perspective may also be used by a rancher who identifies drought as when a particular pond or stream dries up.

Socio-economic Drought Perspective

Not all water shortages are manifest in ways that impact people. A socio-economic perspective does not recognize drought until it tangibly effects peoples' lives in terms of their behavior and options (e.g., water rationing, increased prices, or lost recreational opportunities) or depressed earning power (in particular reduced agricultural income which may effect the viability of the individual enterprise and, if severe enough, may trickle down and adversely affect through other industries, thus increasing regional financial stress).

Drought Perspective Complications

These 4 perspectives—meteorological, agricultural, hydrologic, and socio-economic—are frequently out of phase; therefore, contradictory statements in discussions about drought are not surprising. Differing definitions and perspectives result in confusion and make it difficult for people with diverse interests to agree about what a drought is, when it begins, and when it ends. Meteorologic drought is not directly tied to agricultural drought because other factors—such as temperature, wind, infiltration rate, soil moisture storage capability, timing of rain relative to plant growth needs—are not accounted for in the definition of meteorologic drought, but do make a difference in the perception and consequences of agricultural drought. The beginning and end of a hydrologic drought, especially when viewed in terms of large reservoir or aquifer management, tends to lag far behind meteorologic drought. Also, depending on the recharge system, hydrologic drought is less closely associated with total amount of precipitation than to episodic large events which generate significant runoff or deep drainage. Thus, a single high-intensity thunderstorm may produce a flash-flood that fills reservoirs and exceeds the monthly precipitation average, but does little to alleviate a water shortage for terrestrial vegetation. Conversely, a series of light showers may result in lush plant growth, but not recharge streams and aquifers.

The socio-economic elements of drought are especially complicated because there is a human expectation element involved that may or may not be realistic. For example, the demand for water may be impossible to fulfill when regional economic development expands demand beyond typically available supplies. Thus, water availability during a dry period might not be recognized as drought in sparsely settled areas, but could result in serious water shortages if a large urban population were present. Likewise, a pastoralist who grazes a cattle herd may experience the consequences of drought sooner and more frequently than a pastoralist herding camels.

The socio-economic ripple-effects (secondary impacts) initiated by a water shortage make it very difficult for diverse stakeholders to agree about when the consequences of a drought have ended (Kulshreshtha and Klein 1989). For example, a water shortage that reduces crop and fodder growth may force ranchers to sell their livestock. Once livestock are sold, it may take several years to build herds back to their original pre-drought level. Ultimately, a reduction in income may lead to the financial demise of some enterprises, contributing to migration out of the region. For example, about 250,000 people who had settled on the U.S. prairies during the high rainfall years early in the century left their homesteads during the 1930's drought, never to return (McKay 1980).

The Drought Paradox

A common worldwide assertion by users of degraded rangeland is that droughts are more frequent and more severe than during previous generations. However, there is usually no discernable difference in the long-term trend of the amount and temporal distribution of precipitation and/or temperature. How can these seemingly contradictory observations be reconciled?

Despite no widespread conclusive evidence that "meteorological" droughts are increasing, a history of unsustainable range use causes an increase in the frequency and consequences of drought defined from an "agriculture perspective". The increase in "agricultural" drought is attributable to erosion, crusting, and/or degraded vegetation.

Erosion

Semi-arid rangelands are highly susceptible to erosion (Marshall 1973, Mannering 1981). This is because wet environments have sufficient rainfall to support a natural vegetation cover capable of protecting the soil from the erosive energy of wind and water; and arid environments generally have insufficient rainfall and runoff to transport large quantities of sediment. In semi-arid regions, extreme or intense precipitation events do occur which can transport large quantities of sediment, yet cover needed to protect the soil from wind and water erosion is not complete. The erosion hazard during a drought is increased when prolonged grazing pressure has further reduced plant cover. Wind velocity, and its potential to detach and transport dry soil, exponentially increases near the ground as vegetation's sheltering effect is reduced (Marshall 1973). Substantial nutrient loss is often associated with wind erosion. For example, Bennett (1939) found that the organic matter and nitrogen content of soil suspended by wind was 3 times greater than in the soil left behind.

For many western U.S. rangelands, an erosion rate of about 1 mm yr^{-1} (approximately 11 tons ha^{-1} yr^{-1}) is considered an "acceptable" soil loss rate (Mannering 1981). This interpretation of "acceptable" is at odds with the very slow rate of soil formation on rangelands, which is usually much less than the 0.1 mm yr^{-1} rate of soil formation estimate for cropland (Pimental et al. 1976, Pimental et al. 1995). Part of the reason for the discrepancy between soil formation and erosion rates is that "acceptable" is a subjective term that is influenced by the extent of the planning horizon (e.g., planning to maintain production potential for a 50 year period results in a quite different "acceptable" erosion rate than if planning over a 500 year horizon). Due to the long-term loss of soil depth and its associated decline in water storage potential, adoption of a zero-level accelerated erosion standard for rangelands has been recommended as a management criterion which aims to maintain and enhance site productivity (Mannering 1981). Accelerated erosion is soil loss caused by human land use decisions, as contrasted with natural or geologic erosion which occurs independent of human activities.

The danger of rangeland use resulting in accelerated erosion that would threaten long-term sustainability was addressed by the Society for Range Management Task Group on Unit in Concepts and Terminology (1995) which recognized that sustainability (the fundamental goal of rangeland management) depends primarily on conservation of the soil. This group concluded that erosion was a function of protective attributes (e.g., cover, biomass, density of plants), therefore use of the rangeland should not contribute to reducing the protective attributes of vegetation below a level identified as the Site Conservation Threshold (SCT) (i.e., the point beyond which vegetation is unable to hold the soil in place).

On rangelands where accelerated erosion is occurring, the gradual decrease in soil depth translates into a loss of soil moisture storage capability which, in turn, can increase both the frequency and length of periods without enough soil moisture for expected plant growth. As a site becomes increasingly vulnerable to agricultural drought, the difficulty in maintaining plant cover increases and the site becomes more vulnerable to accelerated erosion, which creates a spiral of decreasing production potential (Thurow 1991, Le Houérou 1996). Indeed, one definition of desertification is the diminution or destruction of biological production potential (Dregne 1987), a characterization that is not specifically linked to precipitation. Therefore, even though precipitation patterns do not change, a site can lose production potential by losing soil which reduces the nutrients and moisture storage capability of the site.

Crusting

Another problem associated with a site's vegetation cover dropping below the site conservation threshold (SCT) is that the exposed soil has an increased susceptibility to crusting. When rain strikes exposed soil the particles are detached by the raindrop energy and are likely to lodge in the remaining soil pores, making them smaller or sealing them completely (Lynch and Bragg 1985). This is one way in which soil crusts are formed. A "washed in" layer of clay particles that clogs soil pores and forms a crust may reduce infiltration rates by up to 90% (Boyle et al. 1989).

An increase in grazing intensity is sometimes advocated as a stop-gap measure intended to increase infiltration (OTA 1982). Livestock trampling does break soil crusts and incorporate mulch and seeds into the soil; however, this prescription is not a solution since any increase in infiltration is short-lived because the raindrop impact quickly reseals the soil surface as the unstable soil pores become plugged. The potential for wind erosion also increases when the soil has been churned to dust. The only solution to crusted soils is to eventually accumulate enough cover so that rainfall energy is dissipated before it reaches the soil. Building back the cover may be a very slow process; like with many aspects of degradation, it is much easier to avoid getting into the problem than trying to fix it.

Degraded vegetation

Many perceived agricultural droughts are related to forage shortages which should be recognized as carrying capacity crises caused by inappropriate stocking policies (Robinson 1982, Dankwerts and King 1984). Numerous studies support the general conclusion that there are no significant differences in infiltration rates or soil loss between similar ungrazed and moderately grazed rangelands (cf., Thurow 1991). However, heavy grazing results in reduced infiltration and accelerated erosion. The quandary is that moderate grazing rates are, in practice, calculated on the basis of expected production from a site. During an agricultural drought, the physiological needs of forage plants are not met and production rapidly declines. The result is that rangelands stocked at a moderate rate based on long-term experience may actually be heavily stocked based on physiological condition of plants during a dry period. Physiological stress may occur more quickly if the vegetation has low energy reserves as a result of having been subjected to intense grazing pressure prior to a dry period. The amount, vigor, and quality of vegetation is correlated with the condition of the range. Therefore, agricultural drought on sites in poor condition is likely to be manifest more frequently and more severely than on sites in good condition.

Figure 1 illustrates the decline in the stocking rate on the Texas Agriculture Experiment Station at Sonora since the site was obtained by the State in 1916. Throughout this period, managers of the ranch considered it to be moderately stocked. Productivity has demonstrably declined to the point that it would now by physically impossible to keep the same number of livestock alive (much less in productive condition) on the same rangeland that once supported higher stocking rates for decades. Two factors have probably contributed to this condition. One is an increase of low palatability woody shrubs which have a high water use potential (e.g., *Juniperus pinchotti* Sudw.) (Smeins et al. 1997). and another is erosion of the shallow (~25 cm) silty-clay (overlying a fractured limestock substrate) which has reduced the site's water-holding capacity. Indeed, it is a common assertion in the region that frequency of drought is increasing and carrying capacity is decreasing, even though no statistical difference in the monthly or annual precipitation or temperature has occurred. The degree to which the decrease in stocking rate and perception of drought are attributable to reduced soil moisture storage capability is complicated by the fact that erosion and infiltration are related to composition shifts in vegetation cover which

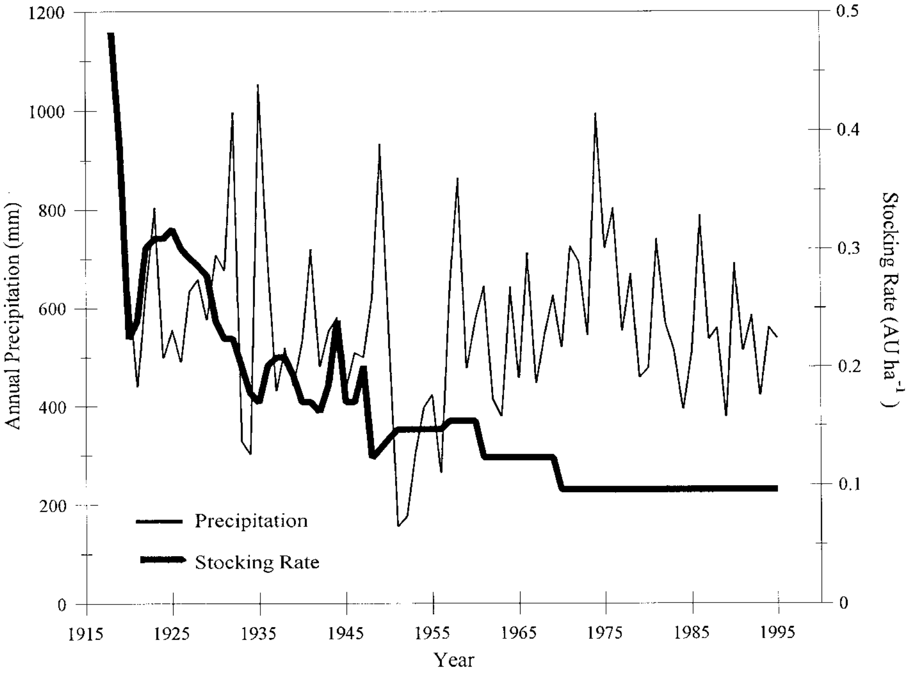

Fig. 1. Stocking rate and precipitation records for the Texas A&M University Sonora Research Station.

may be less palatable to livestock and/or increase the rate of evapotranspiration loss from the site (Thurow et all 1986, Thurow and Hester 1997).

In extreme cases of widespread rangeland degradation, a severe reduction of vegetation cover can change surface reflectivity, which can theoretically inhibit cloud formation and reduce precipitation (Charney et al. 1975, Otterman 1977). For managers to prevent accelerated erosion and possible alteration of local climate, their management system must be able to respond to reduced vegetative growth quickly, so that adequate plant and litter cover remain (i.e., so that the SCT is not crossed).

The Role of Government in Drought Response

Lowdermilk's (1953) classic review of civilization and natural resource use concluded that preservation of the soil resource and associated hydrologic conditions are essential to a society's well-being. Lowdermilk cautioned that history illustrates how decisions made for short-term economic and political reasons are the root cause of long-term degradation. Such concerns are especially manifest when the long-term threat of erosion is pushed to the background in response to short-term pain associated with a drought. Placing erosion control as top priority in such circumstances is unlikely because this issue for politicians "is thorny, it is packed with political dynamite, and it will always keep for another couple of years" (Huxley 1937).

Droughts are a natural part of climate and are certain to occur; therefore, droughts should be expected. It is disingenuous to use the unpredictability of drought as an excuse for inadequate planning decisions that have failed to take rainfall variability into account! Exposing the land to accelerated erosion hazard should be viewed as a managerial failure, instead of making drought a scapegoat for faulty policies.

One reason that policy-makers and landowners persist in treating drought as a quirk of nature is that if they accept the challenge of planning for drought, then they implicitly accept the responsibilities associated with the development and implementation of proactive responses to drought. These are difficult responsibilities to bear because the costs of planning for drought are fixed and occur now while the costs of degradation from drought are uncertain and occur later.

Due to a general failure to include drought as part of the policy formulation process, "post-drought assessments and evaluations have generally shown governmental response to drought is largely ineffective, poorly coordinated, untimely and economically inefficient" (Wilhite 1987). An example of the negative impacts of governmental responses to drought on rangelands is the USDA-FSA Emergency Feed Program which has recently been phased out and is being replaced with the Non-Insured Assistance Program. These kinds of programs, by any name, enable ranchers to stock at higher rates than would be prudent if they were vulnerable to the full downside risk associated with drought.

"Moral hazard" is a term used to describe a policy that encourages reckless behavior because the participants know they will be buffered from negative consequences (Fleisher 1990). Feed assistance programs create a moral hazard because a rancher is positioned to benefit from maintaining a high stocking rate if the rains resume and the government reduces or eliminates the potential for short-term financial losses if the drought continues. Pastoralists in countries with governments unlikely to intervene with financial aid are typically conservative and risk averse. The example of an acrobat who is much less daring when there is no safety net illustrates that behavior changes as a function of available risk protection. Knowing that the government will provide a feed subsidy "safety net" during drought makes non-sustainable stocking rates appear more profitable than lower stocking rates in the short-term (Holechek and Hess 1995). These types of feed subsidy programs undercut the linkage between ecology and economics.

Ironically, government programs to provide "drought relief" feed subsidies enable managers to retain livestock on rangelands longer into a drought, thereby increasing the potential for degradation of the soil and vegetation resource which will actually increase the frequency and consequences of an agriculture drought. Rather than subsidize feed, government policies should focus on providing incentives for early destocking in response to dry conditions. Incentives geared to facilitating early destocking would be especially helpful in moderating damage to leased lands. This is because lease fees tend to be based on a land unit, instead of a per-head basis. Under these conditions, the leasee tends to have a low equity position in livestock and may not be able to sell them without being forced into bankruptcy.

If politicians remain intent on providing feed subsidies, access should be combined with a requirement that ranchers tangibly demonstrate that they are practicing effective grazing and business management. This could be accomplished by requiring that ranchers implement a drought response strategy, pre-approved by an organization such as the USDA-NRCS, as soon as forage production begins to lag behind expectations. Qualification for subsidies would be limited to ranchers who receive pre-approval for their plan and document that they were implementing the plan. Rancher-targeted courses in grazing and financial management would help in the development of ranch-specific drought response plans. In this way government programs would serve mostly as sources of information that will help to reduce environmental and financial risk. Such programming may be considered over obtrusive by some, but the program would be voluntary and would reward good stewardship instead of poor management. The key is that accountability for sound environmental management be built into a feed subsidy program.

Another consideration for government-sponsored drought relief would be the initiation of a long-term easement program, similar to the Conservation Reserve Program (CRP), designed to facilitate resting rangeland in an area designated as being affected by drought. Under such a program a rancher would receive payments for removing livestock for the duration of the drought and for a specified period thereafter. Historically, it has taken a region months or years for herds to recover to pre-drought levels. Gradual re-stocking gave range plants a chance to recover once the rains resumed. Such a scenario is no longer likely, especially since improved transportation networks and the North American Free Trade Agreement (NAFTA) has expanded the area from which to draw livestock to rapidly restock rangeland.

The Role of the Rancher in Drought Response

There will always be uncertainty (imperfect knowledge) regarding inherent climatic variability, market prices, and external financial considerations such as interest rates. Planning for drought must, therefore, focus on things that the manager can do to reduce risk (uncertain consequences) associated with climatic variability.

Devising a management strategy that emphasizes minimizing climatic and financial risk is a more sound approach to ranch management than attempting to maximize forage production and harvest efficiency (Holechek 1996). Ranches that employ intensive grazing systems geared to maximizing harvest efficiency often encounter a "feed-drought" sooner and more frequently than a ranch with lower harvest efficiency (Holechek 1993). Use of intensive grazing systems requires the rancher to promptly respond to deviations from expected forage supply. Such an expectation is simply not realistic for many ranchers since they do not have the labor availability, the mindset, or the ecological/financial expertise to implement this responsibility.

Modern technology and financial structures provide many self-evident benefits in terms of increasing efficiency and flexibility of rangeland use. However, this flexibility can be misapplied to enable ranchers to delay making de-stocking decisions. For example, the ability to procure loans for feed supplies can allow a rancher to retain livestock on the range past the point of rangeland carrying capacity. Development of wells provides a secure water source, thereby the natural controlling factor of drinking water availability is de-coupled from forage availability (Sandford 1983). As a result of the delay afforded by ranch improvements, decisions intended to reduce short-term losses can actually raise the stakes by increasing long-term economic and ecological risks, including the possibility for catastrophic damage (i.e., bankruptcy from an economic perspective and irreversible degradation from an ecological perspective), if the hoped-for rain does not occur.

In the absence of moral hazard behavior encouraged by subsidies, the economic optimum (maximum profit) stocking rate is almost always lower (and never higher) than the biological optimum (maximum sustained yield) (Workman 1986). It is therefore vital that the rancher maintain the proper stocking rate for any given weather/forage condition to minimize the consequences of drought. If ranchers aggressively implement tactical decisions of substantial destocking they will have better long-term expected economic return, with less variance, than if they engage in hopeful inaction (Stafford Smith and Foran 1992). This conclusion, based on an analysis of a sheep enterprise on the semi-arid rangelands of South Australia, showed that a policy of aggressive destocking when rain begins to lag behind expectation would have been the most economically rewarding and sustainable course of action, given commodity price responses and using weather records of the past century. Likewise, an analysis of arid zone beef cattle ranches in central Australia over the past century (Foran and Stafford Smith 1991) concludes that if no government support was available during dry years, then a low-stocking strategy was favored, but that availability of government support during drought made strategies with higher stocking more favorable.

It is the responsibility of the individual rancher to be aware of how much forage is available and to anticipate current and future animal (livestock and wildlife) demand. Monitoring the extent of use on key vegetation species is a useful indicator of grazing pressure. By careful monitoring and control of grazing, the rancher can quickly identify and respond to the beginning of a forage deficit. User-friendly computer decision aids, such as The Grazing Manager (Kothmann and Hinnant 1992) or the Grazing Lands Application (GLA)/Resource System Planning Model (RSPM) Stuth et al. 1990) have been developed to help ranchers estimate seasonal adjustments of livestock stocking rates and test "what if" scenarios regarding rainfall. These tools provide the rancher with timely information to maintain a proper balance between forage production and animal demand, thus preventing damage to the range resource, limiting death losses of livestock due to consumption of poisonous plants (Taylor and Ralphs 1992) and avoiding the full vulnerability associated with market crashes that frequently accompany droughts. Adoption of a grazing strategy that provides a cushion of "reserve forage" provides ranchers some flexibility in the speed and extent to which they must respond to drought. Another reason that lower stocking rates are usually more desirable than seeking to maximize harvest efficiency is to allow for the periodic use of fire necessary to control brush encroachment (Taylor and Kothmann 1993).

The wait-and-see management style that characterizes the majority of rangeland use decisions in the face of drought has a high long-term cost, especially in terms of the irreversible costs of erosion. The downward spiral is self-perpetuating: as erosion occurs there is less soil moisture storage capability and more production vulnerability to inherently erratic precipitation patterns. Rather than blaming management problems on climate, the challenge to rangeland scientists and policy-makers is to intensify the research focus on crafting and implementing management and policy tools designed to better integrate the economic and ecological aspects of drought-induced de-stocking decisions.

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52:420–430 September 1999

Land use change effects on breeding bird community composition

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Abstract

We identified land uses, vegetation cover types, and landscape patterns associated with avian community diversity in 2 rural landscapes in a hardwood forest-tallgrass prairie ecotone that differ with regard to human population density. We obtained long-term (24 years) changes in avian community composition through records from the North American Breeding Bird Survey. We obtained historical and present land use, vegetation cover types, and landscape structure of both landscapes from high-resolution aerial photography. Avian community composition in the low density rural population landscape was primarily related to the amount of land in deciduous forest and land treated with fire or herbicides. In contrast, avian community composition in the high density rural population landscape was primarily related to the amount of land in deciduous forest, native grassland, and roads. Changes in vegetation cover type were related to changes in the avian community composition by increasing prairie habitat associated species in the low density rural population and generalist habitat associated species in the high density rural population landscapes. Loss of neotropical migrants and increased number of generalist species in the high density rural population landscape was related to decreased native vegetation, road development, and increased landscape fragmentation. Biologists and conservationists in this region should focus attention on preserving biological diversity of rural ecosystems by maintaining native plant communities.

Key Words: Agriculture, avian species, landscape structure, urbanization, vegetation cover type

Resumen

Identificamos los usos de la tierra, tipos de cobertura vegetal y patrones del paisaje asociados con la diversidad de la comunidad de aves de dos paisajes rurales en un ecotono de bosque de madera dura - pradera de pastos altos que difieren respecto a la densidad de población humana. A través de los registros del North American Breeding Bird Survey obtuvimos los cambios a largo plazo de la composición de la comunidad de aves. Mediante el uso de fotografía aérea de alta resolución obtuvimos el uso histórico y presente de la tierra, tipos de cobertura vegetal y estructura del paisaje en ambos tipos de paisaje. En el paisaje de baja densidad de población rural, la composición de la comunidad de aves estuvo relacionada principalmente a la cantidad de tierra en el bosque deciduo y al terreno tratado con fuego o herbicidas. En contraste, la composición de la comunidad de aves del paisaje alta densidad de población rural se relaciono principalmente a la cantidad de bosque deciduo, pastizal nativo y caminos. Los cambios de tipo de cobertura vegetal se relacionaron con cambios en la composición de la comunidad de aves, en las áreas de baja densidad de población rural mediante un incremento de especies cuyo hábitat es la pradera y en las áreas de alta densidad de población rural por el aumento de especies generalistas. La perdida de especies neotropicales migrantes y el aumento de especies generalistas registrada en el paisaje de alta densidad de población rural se relaciono con la reducción de la vegetación nativa, desarrollo de caminos y el aumento en la fragmentación del paisaje. Los biólogos y conservacionistas de esta región deben enfocar su atención en preservar la diversidad biológica de los ecosistemas rurales mediante el mantenimiento de comunidades de plantas nativas.

Land use intensification often reduces ecosystem diversity on a regional scale due to the replacement of natural vegetation with managed systems of altered structure (Davis and Glick 1978, Krummel et al. 1987). These anthropogenic changes have caused concern about preserving and managing biological diversity (Grove and Hohmann 1992, Urban et al. 1992, West 1993). Management of avian diversity in urban environments has become increasingly important because of increasing urbanization, growth in non-consumptive uses, and economic returns of urban wildlife (Gill and Bonnett 1973, DeGraaf and Payne 1975, Smith 1975, George 1982). Although the effects of urbanization on many wildlife species are well documented, the dynamics of heterogeneous environments, such as the wildland to suburban ecotone, have been largely ignored by ecologists. As the human population expands, more emphasis should be placed on maintaining

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This study was approved for publication by the Director, Oklahoma Agricultural Experiment Station and funded in part by the Oklahoma Agricultural Experiment Station through project S-1822 and a grant from the Targeted Research Initiative Program.

Manuscript accepted 13 Nov. 1998.

avian biodiversity to protect desirable species (Rodiek 1991). However, few studies have compared the avifauna and vegetation of urban areas with the outlying, less intensively used areas (Beissinger and Osborne 1982).

The relationship between vegetation cover types, habitat structure, and avian communities is useful for examining effects of land use on breeding birds at both stand and landscape level and should be addressed when assessing habitat quality (DeGraaf 1991, Scott et al. 1993). However, most population surveys of avian species have been at spatial scales of about 40 ha and in monocultures (Urban and Shugart 1984). Therefore, habitat management to maintain high historical diversity of avian species depends on the knowledge of changes that can or will occur in a given landscape because the landscape is a mosaic of stands and local ecosystems (DeGraaf 1991).

Implications of increasing human activity on the avifauna in the hardwood forest-tallgrass prairie ecotone must largely be extrapolated from previous studies conducted in contiguous forests (Johnson and Temple 1986). However, native birds in North America's prairies have undergone more widespread declines over the past 25 years than any other U.S. bird group, which warrants the increasing concern for the conservation of these birds (Knopf 1994). Therefore, we chose 2 rural landscapes in northern Oklahoma that differed in human population density to test the hypothesis that human activity alters avian community structure in a hardwood forest-tallgrass prairie ecotone. Specifically, we hypothesized that 1) avian community composition in a high density, rural population and a low density, rural population landscape differed in 1966 and diverged over time as the high density rural population landscape became more urbanized, and 2) different vegetation cover types between the landscapes, in part reflecting different human activities and agricultural practices, influenced avian community composition.

Study Site

Our study was centered around suburban Tulsa, Okla., and included the surrounding rural areas in northeastern Osage and southern Washington counties. We selected 2 U.S. Fish and Wildlife Service Breeding Bird Survey routes, 024 (Collinsville) and 026 (Bartlesville) (Baumgartner and Baumgartner 1992), within the ecotonal area of the Cherokee Prairie grassland formation and oak (*Quercus* spp.)-hickory (*Carya* spp.) savanna of the Cross Timbers (Bruner 1931, Soil Conservation Service 1981). The Cherokee Prairie of Oklahoma extends as a long narrow strip, 240 km southward from the Kansas state line with a width of 50–100 km throughout most of its length. The strip is better adapted to support grasses, forbs, and legumes than forests because of climate and underlying geology (Harlan 1957). The Cross Timbers lie west of the Cherokee Prairie and the Lower Arkansas Valley, extending 290 km southward from Kansas with a width of 80 km wide. The region is a transitional oak forest with interspersed prairie (Bruner 1931, Gray and Galloway 1959).

Survey routes also varied in their proximity from Tulsa, a major metropolitan area in northern Oklahoma with an estimated population of 361,628 (U.S. Department of Commerce 1990). The Collinsville route is located in Washington County and the Bartlesville route is located in Osage County. A 50% increase in human use areas was observed in the Collinsville route while a 4% decrease was observed in the Bartlesville route between 1966 and 1990 (Boren et al. 1997). Human population density of Washington and Osage County in 1990 was 3,340 km^{-2} and 520 km^{-2}, respectively. In addition, rural population density differed between the 2 routes. Rural population density of Washington and Osage County in 1990 was 10.3 km^{-2} and 4.9 km^{-2}, respectively. Rural population is defined the by U.S. Department of Commerce (1990) as residing in communities of less than 2,500 people. Hence, from this point forward, the 2 landscapes will be discussed as high density rural population or low density rural population. Each landscape includes the breeding bird survey route (40.2 km in length) and 0.8-km on each side of the route boundary. The resulting coverage was approximately 6,430 ha for each landscape.

Methods

Bird Surveys and Database Construction

We used breeding bird survey routes from the U.S. Fish and Wildlife Service to obtain our avian diversity data. The U.S. Fish and Wildlife Service Breeding Bird Survey is the only data set that indexes the population status of many species of birds over a large geographical area and time (Bystrak 1981, Geissler and Noon 1981). Although a roadside count misses some species and is limited by road placement, the results are considered to be fairly reliable indexes for a prairie-woodland ecosystem (Baumgartner and Baumgartner 1992).

We classified avian species as neotropical migrants, temperate migrants, and residents and grouped species into 5 designations of habitat occurrence: forest, forest edge and shrubland, prairie, wetland, and developed areas. We further grouped species into foraging zones: aerial (open zones), ground and shrub (foliage 0–3 m), midstory (foliage 3–10 m), canopy (foliage > 10 m), bole (trunks and limbs), and water. Nesting zones included ground, shrub (0–3 m), midstory (3–10 m), canopy (> 10 m), cavity, and other (variable heights and substrates). Classification of avian species was adapted from Harrison (1975), Bull and Farrand (1988), and Hamel (1992).

Bird abundances from 1967 to 1991 were segregated around 4 years (1966, 1973, 1980, and 1990) for which vegetation cover type and landscape structure data were documented from a previous study for both landscapes (Boren et al. 1997). Thus, breeding bird data from 1967 to 1970 corresponded to the 1966 landscape data, breeding bird survey data from 1971 to 1976 corresponded to the 1973 landscape data, breeding bird survey data from 1977 to 1984 corresponded to the 1980 landscape data, and breeding bird survey data from 1985 to 1991 corresponded to the 1990 landscape data. Relative abundance was then calculated for each of the 4 time periods by averaging relative abundance for the 4 years. Landscape data included land use and vegetation cover types (Table 1), and landscape structure measures included mean patch size, fractal dimension, landscape richness, Shannon diversity, dominance, contagion, and angular second moment (Boren et al. 1997).

Table 1. Classification system used to map vegetation cover types (adapted from Stoms et al. 1983).

Land use and cover type	Description
Developed area	Land occupied by residential, industrial, or other human structures and non-agricultural activities. Also includes transportation and utility facilities.
Roads	Black top, gravel, dirt roads, and driveways
Water	Ponds, lakes, streams, and rivers
Cropland	Land cultivated for row crops and cereal grains but excluding grazing lands
Pasture land and hay meadows	Includes pasture land (seeded grasslands used for grazing by cattle, sheep, goats, and horses) and hay meadows
Native grassland	Native grasslands with less than 10% cover by shrubs or trees
Scrub forest	Vegetation dominated (>10%) by cover of broadleaf hardwoods. Mostly post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*)
Brush-treated land	Native vegetation subjected to herbicides, fire, or chaining to control woody brush encroachment
Bare ground	Land with less than 5% vegetation cover

Data Analysis

Avian Community Change

We performed detrended correspondence analysis (DCA) with the program CANOCO (ter Braak 1988) to determine if avian community composition differed between landscapes and to document shifts in avian community composition over time by using year as the passive environmental variable. Detrended correspondence analysis is an indirect gradient analysis in which samples (species abundances) are arranged according to species composition alone. The important environmental gradients are indirectly inferred from the trends in species abundances. The first 2 axes of the DCA ordination were selected as the main ordination framework because higher eigenvalues indicate more importance in explaining avian community variability (Table 2). Detrended correspondence analysis has the advantage of producing axes that correspond to actual ecological distances, as defined by the abundance of species, and are not forced to be equal in length (Malanson and Trabaud 1987). We plotted the centroids for avian community composition for individual years in DCA space as points. We used these points to indicate trajectories through time in the avian space defined by the ordination axes (Whisenant and Wagstaff 1991).

We used species scores generated by DCA to determine the avian species responsible for temporal shifts in avian community composition. Visual observation of axis 1 and 2 of the ordination diagram indicated bird species (with overall abundances > 3) most responsible for temporal change in avian community composition. Therefore, DCA provided a multivariate approach to identify species that were declining or increasing within each landscape.

Influence of Landscape Cover Type and Structure

We performed canonical correspondence analysis (CCA) with the program CANOCO (ter Braak 1988) to determine the influence of vegetation cover type and landscape structure on the breeding bird community for each landscape. Canonical correspondence analysis is an eigenvector ordination technique for multivariate direct gradient analysis (ter Braak 1986). This technique explains community variation by detecting patterns of variation in species abundance that can best be explained by a set of environmental variables (ter Braak 1986). By applying CCA, it is possible to identify important environmental variables that explained avian community composition with no *a priori* knowledge about possible predictor variables (Saetersdal and Birks 1993).

We related abundances of all bird species in the high density rural population and low density rural population landscapes (100 and 86 bird species, respectively) to both vegetation cover type and landscape structure variables in separate CCA ordinations. We used forward selection and Monte Carlo permutation tests ($P < 0.05$) to determine environmental variables that best explained variation in breeding bird abundances. We examined canonical coefficients and intraset correlations to evaluate relative contributions of environmental variables to the axes. We also used unrestricted Monte Carlo permutation tests for statistical significance ($P < 0.05$) of the first 2 ordination axes. Tests of significance in CCA do not depend on parametric distributional assumptions; therefore, we did not transform species and environmental variables (Palmer 1993).

Canonical correspondence analysis biplots provided weighted least squares approximations of the weighted averages of species identified as causing shifts in community structure (from DCA) with respect to environmental variables (ter Braak 1986). We examined bird species relationships with a given environmental variable by continuing the environmental variable line through the origin in the biplot. A perpendicular line was then dropped from each bird species position to the variable of interest. Endpoints of the perpendicular line indicate relative positions of bird species distribution centers along the environmental variable. These endpoints indicate relative relationship of each species to a given variable (ter Braak 1986, 1987).

We used CCA with year as the only environmental axis to plot species scores of the high density rural popula-

Table 2. Eigenvalues and cumulative variance (%) of species data for the first 4 axes of detrended correspondence analysis on species data, with year as a passive environmental variable, in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Low density rural population					
Eigenvalue	0.30	0.22	0.12	0.09	2.73
Cumulative variance of species data (%)	11.1	18.9	23.5	26.9	
High density rural population					
Eigenvalue	0.38	0.18	0.12	0.09	2.91
Cumulative variance of species data (%)	12.9	18.9	23.2	26.4	

Table 3. Temporal changes in vegetation cover types (ha) and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990 (Boren et al. 1997).

Index	Year				Change
	1966	1973	1980	1990	
High density rural population (Collinsville)	- - - - - - - - - - - -	(ha)	- - - - - - - - - - - - -		(%)
Developed areas	16	7	25	24	50
Roads	88	92	101	87	–1
Water	53	76	58	71	34
Cropland	556	453	208	120	–78
Pasture land and hay meadows	676	672	850	999	48
Native grassland	1,432	1,601	1,546	1,508	5
Deciduous forest	449	294	398	377	–16
Brush–treated land	0	41	4	5	—
Bare ground	2	6	2	2	0
Low density rural population (Bartlesville)					
Developed areas	23	18	16	22	–4
Roads	108	94	121	118	9
Water	27	39	30	38	41
Cropland	25	41	12	13	–48
Pasture land and hay meadows	90	50	25	49	–46
Native grassland	1,375	1,308	1,120	1,117	–19
Deciduous forest	1,184	980	950	887	–26
Brush–treated land	397	616	877	878	121
Bare ground	20	7	10	8	–60

tion landscape against the low density rural population landscape to document divergence of avian communities. If the avian communities of the 2 landscapes were diverging in opposite directions, a negative relationship should exist. In addition, we used CCA with vegetation cover types and landscape structure as covariables and year as environmental variables to measure residual variation. If changes occur over time, some other environmental variables that were not examined in our study were affecting avian community composition.

Results and Discussion

Vegetation Cover Types and Landscape Structure

Differences in human population density and agriculture intensification in these 2 rural landscapes resulted in altered land ownership patterns and management practices that created contrasting vegetation cover types (Table 3) and landscape structure (Table 4) between the low density rural population and high density rural population landscapes (Boren et al. 1997). Land in the high density rural population landscape was subjected to intensive management practices on cropland, pasture land, and hay meadows while land in the low density rural population landscape was predominately in native vegetation that was extensively managed with prescribed burning, herbicide application, and grazing management to increase native grass production for livestock grazing. Measures of mean patch size in our study indicated the high density rural population landscape was 4 times more fragmented than the low density rural population landscape over the entire period (Boren et al. 1997). In addition, the high density rural population landscape became less diverse and more homogeneous while the low density rural population landscape became more diverse since 1966.

Table 4. Measures of landscape structure and percent change from 1966 of high density rural population and low density rural population landscapes in a hardwood forest-tallgrass prairie ecosystem in northern Oklahoma for 1966, 1973, 1980, and 1990 (Boren et al. 1997).

Index	Year				Change
	1966	1973	1980	1990	
High density rural population (Collinsville)	- - - - - - - - - - - -	(ha)	- - - - - - - - - - - - -		(%)
Mean patch size (ha)	4.16	3.93	3.22	2.96	- 29
Fractal dimension	1.23	1.25	1.27	1.28	+ 4
Shannon diversity	1.43	1.39	1.33	1.28	- 11
Dominance	0.65	0.75	0.81	0.86	+ 3
Contagion	2.69	2.83	2.85	2.91	+ 8
Angular second moment	0.27	0.30	0.30	0.32	+ 19
Contrast	0.33	0.46	0.50	0.50	+ 52
Low density rural population (Bartlesville)					
Mean patch size (ha)	3.96	4.29	3.63	3.42	- 8
Fractal dimension	1.27	1.24	1.27	1.30	+ 2
Shannon diversity	1.21	1.29	1.29	1.31	+ 8
Dominance	0.93	0.78	0.78	0.83	- 11
Contagion	2.99	2.82	2.81	2.88	- 4
Angular second moment	0.35	0.30	0.29	0.29	- 17
Contrast	0.41	0.35	0.35	0.42	+ 2

Avian Community Change

The trajectories of points over time (centroids of avian community composition) indicate that the avian community in the high density rural population and low density rural population landscapes diverged along axis 1 and declined along axis 2 (Fig. 1). In addition, the 2 landscapes differ from each other in avian community composition, even ignoring temporal change, which is not surprising considering differences in land use and vegetation cover types between landscapes. The trajectory of both communities progressively diverged over time, but change was greater for the avian community in the low density rural population landscape. Centroid values for the avian community in the low density rural population landscape between 1966 and 1990 changed by 0.42 and 0.20 SD units for axis 1 and 2, respectively. This suggests avian community composition was strongly affected by a temporal decrease in deciduous woodlands by prescribed burning and herbicide application to maintain tallgrass prairie in the low density rural population landscape (Boren et al. 1997). Centroid values for the avian community in the high density rural population landscape between 1966 and 1990 were only 0.20 and 0.20 SD units apart for axis 1 and 2, respectively. Species scores from CCA, with year as the only variable, of the high density rural population landscape had a negative relationship with the species scores of the low density rural population landscape.

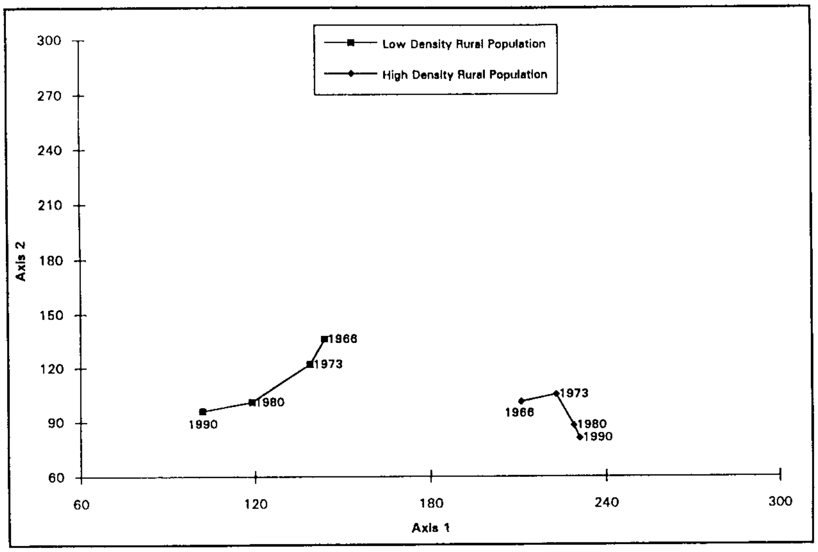

Fig. 1. Detrended correspondence analysis (DCA) ordination of centroids for avian community composition in the low density rural population (extensively managed) and high density rural population (intensively managed) landscapes. Lines indicate trajectories of avian community change between 1966 and 1990 defined by the ordination axes.

This confirms the DCA results that the avian communities were diverging in opposite directions over time (Fig. 2).

Detrended correspondence analysis provides a scaling of axes in units of compositional turnover (SD units; Hill and Gauch 1980). This scaling provides a robust estimate of beta diversity (Okland et al. 1990) that reflects rate of change in community composition along a gradient (Wilson and Mohler 1983, Samson and Knopf 1993). Based on the small SD axis units, both avian communities exhibited low beta diversity with relatively small temporal movement along axis 1 (Fig. 1). Therefore, change or turnover in avian community species composition in the low density rural population and high density rural population landscapes was relatively slow between 1966 and 1990.

Although the avian community in the high density rural population and low density rural population landscapes diverged over time, the great-tailed grackle (*Quiscalus mexicanus*) and rock dove (*Columba livia*) increased in both landscapes (Table 5). This suggests a temporal increase in some generalist species by immigration from nearby source habitats. An aggressive trap and transplant program most likely accounted for the observed increase of wild turkey (*Meleagris gallopavo*) in both landscapes. We observed none of the 10 species endemic to grasslands (Knopf 1994) in our study area. However, grasshopper sparrow (*Ammodramus savannarum*) and dickcissel (*Spiza americana*), secondary species that have exhibited significant declines in grasslands (Knopf 1994), increased in the low density rural population landscape but remained relatively unchanged in the high density rural population landscape. Grasshopper sparrow and dickcissel declines are localized to areas with inadequate breeding habitats (Knopf 1994). The grasshopper sparrow breeds in fields of several types but prefers vegetation about 30 cm tall (Hamel 1992). However, the grasshopper sparrow is sensitive to small changes in its habitat. When herbaceous material becomes too thick or trees encroach on prairies and abandoned fields, these habitats become unsuitable as breeding sites (Bull and Farrand 1988). The dickcissel also requires herbaceous cover (about 60 cm tall) for breeding (Hamel 1992). Therefore, prescribed burning and herbivory related to cattle grazing in the low density rural population landscape favored these species by maintaining breeding habitat. The eastern meadowlark (*Sturnella magna*) and lark sparrow (*Calamospiza melanocorys*), species of high concern, exhibited relatively little change in both landscapes.

The yellow-breasted chat (*Icteria virens*), an edge species of high concern that requires dense thickets and brush for nesting habitat (Bull and Farrand 1988), declined in both landscapes. The conversion of deciduous forests to brush-treated lands in the low density rural population landscape and to pasture land and hay meadows in the high density rural population landscape from 1966 to 1990 (Boren et al. 1997) may account for the decline of this species in both landscapes. The greater prairie chicken (*Tympanuchus capido*) declined only in the high density rural population landscape where brush-treated land accounted for only 1% of the total area (Boren et al. 1997). This species nests in

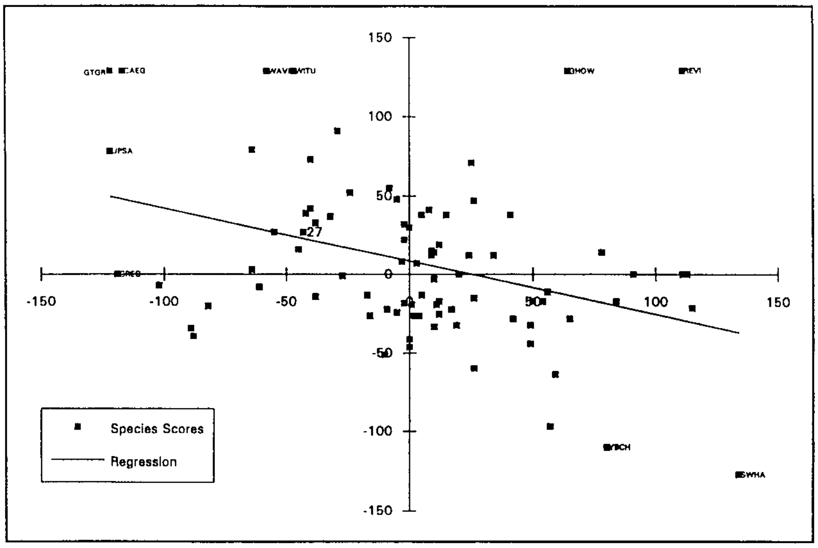

Fig. 2. Species scores from canonical correspondence analysis (CCA), with year as the only variable, of the high density rural population landscape against the plotted species scores of the low density rural population landscape ($r^2 = 0.13$, $P < 0.05$).

Table 5. Avian species responsible for shifts in avian community composition in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape over a 24-year period, 1966 to 1990. Minor species (those that occurred 3 or fewer times) were omitted.

Species	Code	Scientific name	Type[a]	Habitat[b]	Concern[c]	Foraging[d]	Nesting[e]
Low density rural population							
Loss							
Yellow-breasted chat	YBCH	*Icteria virens*	Neotrop	Edge	High	Ground	Shrub
Blue-gray gnatchatcher	BGGN	*Polioptila caerulea*	Neotrop	Edge	Moderate	Canopy	Midstory
Greater roadrunner	GRRO	*Geococcyx californianu*	Resident	Prairie	High	Ground	Shrub
Bewickís wren	BEWR	*Thryomanes bewickii*	Temp	Edge	High	Ground	Cavity
Black and white warbler	BAWW	*Mniotilta varia*	Neotrop	Forest	Moderate	Midstory	Ground
Field sparrow	FISP	*Spizella pusilla*	Temp	Edge	High	Ground	Ground
Painted bunting	PABU	*Passerina ciris*	Neotrop	Edge	High	Ground	Shrub
Pileated woodpecker	PIWO	*Dryocopus pileatus*	Resident	Forest	Moderate	Bole	Cavity
Summer tanager	SUTA	*Piranga rubra*	Neotrop	Forest	High	Midstory	Midstory
Eastern tufted titmouse	ETTI	*Parus bicolor*	Resident	Forest	High	Midstory	Cavity
White-breasted nuthatch	WBNU	*Sitta carolinensis*	Resident	Edge	Moderate	Bole	Cavity
Gain							
Dickcissel	DICK	*Spiza americana*	Neotrop	Prairie	High	Ground	Ground
Wild turkey	WITU	*Meleagris gallopavo*	Resident	Edge	High	Ground	Ground
Barn swallow	BARS	*Hirundo rustica*	Neotrop	Develop	Moderate	Aerial	Other
Grasshopper sparrow	GRSP	*Ammodramus savannarum*	Neotrop	Prairie	High	Ground	Ground
Great-tailed grackle	GTGR	*Quiscalus mexicanus*	Resident	Edge	Moderate	Ground	Shrub
Little blue heron	LBHE	*Egretta caerulea*	Temp	Water	Moderate	Water	Shrub
Rock dove	RODO	*Columba livia*	Resident	Develop	Low	Ground	Other
Black-billed cucko	BBCU	*Coccyzus erythropthaim*	Neotrop	Edge	High	Midstory	Shrub
Cattle egret	CAEG	*Bubulcus ibis*	Resident	Prairie	Low	Ground	Shrub
Yellow-breasted chat	YBCH	*Icteria virens*	Neotrop	Edge	High	Ground	Shrub
Chipping sparrow	CHSP	*Spizella passerina*	Neotrop	Forest	Moderate	Ground	Shrub
Common yellowthroat	COYE	*Geothlypis trichas*	Neotrop	Edge	Moderate	Ground	Shrub
Great-horned Owl	GHOW	*Bubo virginianus*	Resident	Edge	Moderate	Ground	Cavity
Greater prairie chicken	GPCH	*Tympanuchus capido*	Resident	Prairie	High	Ground	Ground
Kentucky warbler	KEWA	*Oporornis formosus*	Neotrop	Forest	High	Ground	Ground
Northern-parula warbler	NOPA	*Parula americana*	Neotrop	Forest	High	Midstory	Canopy
Red-shouldered hawk	RSHA	*Buteo lineatus*	Temp	Edge	Moderate	Ground	Canopy
Yellow-bellied sapsucker	YBSA	*Sphyrapicus sp.*	Temp	Edge	High	Bole	Cavity
Gain							
American robin	AMRO	*Turdus migratorius*	Temp	Develop	Low	Ground	Shrub
Gray catbird	GRCA	*Dumetella carolinensis*	Neotrop	Edge	High	Ground	Shrub
Common grackle	COGR	*Quiscalus quiscula*	Resident	Edge	Low	Ground	Midstory
Great-tailed grackle	GTGR	*Quiscalus mexicanus*	Resident	Edge	Moderate	Ground	Shrub
House sparrow	HOSP	*Passer domesticus*	Resident	Develop	Low	Ground	Cavity
Purple martin	PUMA	*Progne subis*	Neotrop	Develop	Moderate	Aerial	Cavity
Rock dove	RODO	*Columba livia*	Resident	Develop	Low	Ground	Other
European starling	EUST	*Sturnus vulgaris*	Resident	Develop	Low	Ground	Cavity
Wild turkey	WITU	*Meleagris gallopavo*	Resident	Edge	High	Ground	Ground

[a] Species classified as neotropical migrants (Neotrop), temperate migrants (Temp), and residents (Resident) (Bull and Farrand 1988; Hamel 1992).

[b] Species grouped into designations of habitat occurrence: forest (Forest), forest edge and shrubland (Edge), prairie (Prairie), and developed areas (Developed) (Bull and Farrand 1988; Hamel 1992).

[c] Species grouped into population trends: low concern (Low), moderate concern (Moderate), and high concern (High).

[d] Species grouped into foraging zones: open zones (Aerial), foliage 0–3 m (Ground), foliage 3–10 m (Midstory), and trunks and limbs (Bole) (Bull and Farrand 1988; Hamel 1992).

[e] Species grouped into nesting zones: ground (Ground), 0–3 m (Shrub), 3–10 m (Midstory), > 10 m (Canopy), cavity (Cavity), and variable heights and substrates (Other) (Harrison 1975).

habitats of standing residual vegetation from a preceding growing season and is dependent upon stand rejuvenation by fire (Kirsch 1974).

We observed a greater loss of neotropical migrants from the high density rural population landscape compared to the low density rural population landscape (33% and 3%, respectively), which can be attributed to differences in land use and associated management practices. The ratio of neotropical migrants to resident/temperate migrants shifted from 1.2:1 to 0.75:1 in the low density rural population landscape and from 1.2:1 to 0.29:1 in the high density rural population landscape. Changes in neotropical migrant diversity and density by urban sprawl result from human-induced changes in vegetation composition. However, recent scientific studies suggest that the primary factors limiting neotropical migrants are related to fragmentation and edge effect as opposed to habitat loss (Hagan and Johnston 1992, Faaborg et al. 1993, Maurer and Heywood 1993, Thompson et al. 1993).

Landscape quality, especially with regard to landscape fragmentation and diversity, continued to erode between 1966 and 1990 in the high density rural population landscape (Boren et al. 1997), which may account for the observed loss of neotropical migrants from the high density rural population landscape. Problems associated with habitat fragmentation include increased edge habitat, parasitism rates, predation rates, and isolation effects which generally have adverse effects on neotropical migrant species (Johnson and Temple 1986, Faaborg et al. 1993). Our data also suggest that biological diversity and ecological integrity of the high density rural population landscape are lower

Table 6. Eigenvalues, correlation coefficients, and cumulative variances (%) between species and environmental axes for stepwise canonical correspondence analyses carried out on landscape cover type and landscape structure variables in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Vegetation cover type		Landscape structure	
	Axis 1	Axis 2	Axis 1	Axis 2
Low density rural population				
Eigenvalue[a]	0.18	0.12	0.08	0.05
Species-environment correlation[b]	0.80	0.74	0.55	0.55
Cumulative variance explained (%)[c]	43.1	70.6	43.4	68.8
Sum of all canonical eigenvalues[d]	0.43		0.18	
Total inertia	2.74		2.74	
High density rural population				
Eigenvaluea	0.28	0.05	0.09	0.06
Species-environment correlationb	0.88	0.60	0.59	0.52
Cumulative variance explained (%)c	65.1	77.6	41.5	68.2
Sum of all canonical eigenvaluesd	0.44		0.21	
Total inertia	2.91		2.91	

[a] Eigenvalues (λ) measure the importance of the ordination axis.

[b] Species-environment correlation (r) is a measure of how well the extracted variation in community composition can be explained by the environmental variables.

[c] Cumulative percentage variance of species-environment relation.

[d] Sum of all canonical eigenvalues represents the total amount of extracted variation accounted for by the CCA ordination.

compared to the rural landscape. Neotropical migratory birds provide ideal indices of ecological integrity because they are highly sensitive to changes in landscapes that compromise the spatial continuity and integrity of natural ecosystems (Maurer 1993). However, indices of biological diversity must take into account the dynamic nature of ecosystems and include ecological processes occurring outside the area of interest (Landres 1992).

Differences in avian nesting and foraging zones between landscapes can be attributed to differences in land use and associated management practices. Prescribed burning, herbicide application, and grazing management resulted in a 26% reduction of deciduous woodland in the low density rural population landscape (Boren et al. 1997). Avian community in the low density rural population landscape shifted from tree nesting species (55% reduction) to ground and shrub nesters, which supports our observed reduction of tree foraging to ground foraging species in the low density rural population landscape. However, shifts in nesting and foraging zones are not as apparent in the high density rural population landscape. In addition, changes in vegetation cover type was related to changes in the avian community composition by decreasing some forest and edge species in both landscapes relative to prairie and generalist species in the low density rural population and high density rural population landscapes, respectively. Management practices associated with the low density rural population landscape in this study were more conducive to maintaining biodiversity of grassland species. However, community shift towards generalist species in the high density rural population landscape suggest a continued increase in exotics and species beyond their historical range which pose a significant threat to the loss of native avian assemblages (Knopf 1986, Drake et al. 1989).

Influence of Vegetation Cover Type and Landscape Structure

Landscape Cover Type

We expected a strong relationship between vegetation cover types and the distribution of breeding birds (Avery 1989). Indeed, the CCA ordination explained about 43% of the variation associated with the relationship between the vegetation cover types and both the low density rural population and high density rural population avian data sets (Table 6). The eigenvalues for axes 1 and 2 explained 71 and 78% of the cumulative variance of the bird species-landscape cover type relationship, respectively, of the low density rural population and high density rural population data sets. All land-use and vegetation cover types (Table 1) were included in forward selection analysis. Forward selection identified 5 land-use and vegetation cover type variables ($P < 0.05$) that explained 39% of variation in breeding bird abundances in the low density rural population landscape including forest (17%), cropland (9%), water (5%), developed area (4%), brush-treated land (2%), and roads (2%). Forward selection also identified 5 land use and vegetation cover type variables ($P < 0.05$) that explained 38% of variation in breeding bird abundances in the high density rural population landscape including forest (25%), cropland (4%), roads (4%), water (3%), and native grasslands (2%). Both axes were significant ($P < 0.01$) for both landscapes according to Monte Carlo permutation tests.

The relative importance of each environmental variable for predicting the community composition can be found through analysis of canonical coefficients and intraset correlations (ter Braak 1986). Canonical coefficients define the ordination axes as linear combinations of the environmental variables. Intraset correlations are the correlation coefficients between the variables and the axes (ter Braak 1986). Canonical coefficients describe the partial or residual variation and are essentially equivalent to regression coefficients. However, with intraset correlations other variables are assumed to covary with that one environmental variable in the particular way they do in the data set and thus should be used in a multivariate environment. The ordination diagram shows the relationships between the avian community in terms of main axes of variation (Kalkhoven and Opdam 1984).

The variables most correlated with axis 1, based on intraset correlations (Table 7), of the low density rural population landscape were forest and brush-treated land. Thus, axis 1 separated species that decreased and were dependent on deciduous woodland cover [e.g., black and white warbler (*Mniotilta varia*), pileated woodpecker (*Dryocopus pileatus*), summer tanager (*Piranga rubra*), and eastern tufted titmouse (*Parus bicolor*)] from species that increased and required more open canopy and fewer trees (e.g., barn swallow (*Hirundo rustica*), dickcissel, and grasshopper sparrow) (Fig. 3).

The variables most correlated with axis 1 of the high density rural population landscape were forest and native grassland (Table 7). Axis 1 separated forest and shrubland species [e.g., chipping sparrow (*Spizella passerina*), Kentucky warbler (*Oporornis formosus*), and northern parula warbler

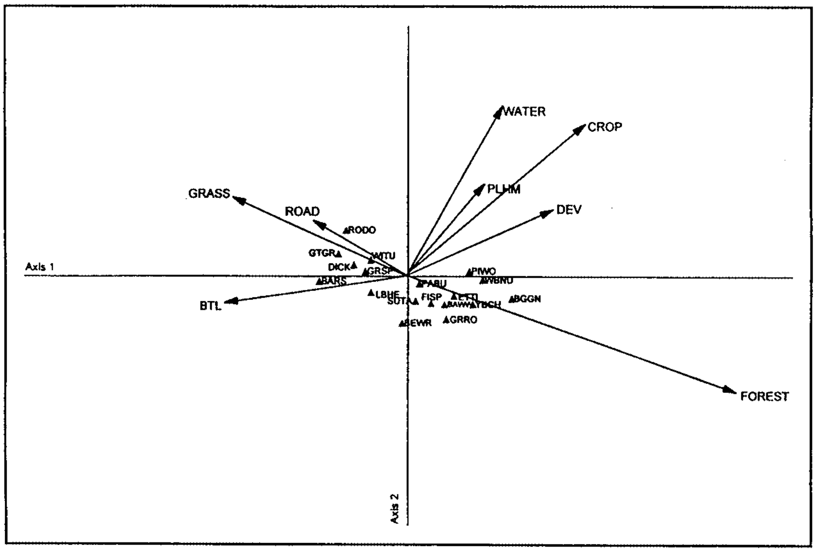

Fig. 3. Distribution of 18 species of birds in the low density rural population (extensively managed) landscape. Canonical correspondence analysis (CCA) ordination diagram with birds (▲) and environmental variables (vegetation cover types; arrows). The bird species are: YBCH = yellow-breasted chat, BGGN = blue-gray gnatchatcher, GRRO = greater roadrunner, BEWR = bewickís wren, BAWW = black and white warbler, FISP = field sparrow, PABU = painted bunting, PIWO = pileated woodpecker, SUTA = summer tanager, ETTI = eastern tufted titmouse, WBNU = white-breasted nuthatch, DICK = dickcissel, WITU = wild turkey, BARS = barn swallow, GRSP = grasshopper sparrow, GTGR = great-tailed grackle, LBHE = little blue heron, and RODO = rock dove. Environmental variables are: DEV = developed area, ROAD = road, WATER = water, CROP = cropland, PLHM = pasture land and hay meadows, GRASS = native grassland, FOREST = scrub forest, and BTL = brush-treated land.

(*Parula americana*)] from species preferring open grasslands (e.g., greater prairie chicken) (Fig. 4). Roads and grassland were most correlated with axis 2 of the high density rural population landscape. Axis 2 separated generalist species that increased and are commonly associated with human development [e.g., American robin (*Turdus migratorius*), house sparrow (*Passer domesticus*), purple martin (*Progne subis*), rock dove, and European starling (*Sturnus vulgaris*)] from prairie species which declined and are associated with less human disturbance [e.g., greater prairie chicken and cattle egret (*Bubulcus ibis*)] (Fig. 4).

Different vegetation cover types between the landscapes influenced avian community composition in this study. Avian community composition was primarily related to deciduous forest and brush-treated land in the low density rural population landscape compared to deciduous forest, native grassland, and roads in the high density rural population landscape. Continued urban sprawl into rural landscapes may result in increased generalist species as the result of increased roads and decreased native grassland. However, inferences on the influence of urban sprawl on rural avifauna must be made with caution. High mobility of birds makes them less dependent on local conditions than sedentary species and avian community composition may be influenced by surrounding bird communities (Jarvinen and Vaisanen 1980).

Landscape Structure

The CCA ordination explained approximately 18 and 21% of the variation associated with the relationship between the landscape structure and the low density rural population and high density rural population avian data sets, respectively (Table 6). Because vegetation cover types explained more than twice the variation of the avian data set compared to the landscape structure variables, vegetation cover type ordinations better explain temporal changes in avian community composition in this study. At the landscape scale, avian community composition is a function of vegetation structure (physiognomy) while at the within-stand level, particular plant taxonomic composition (floristics) is more important than structure in

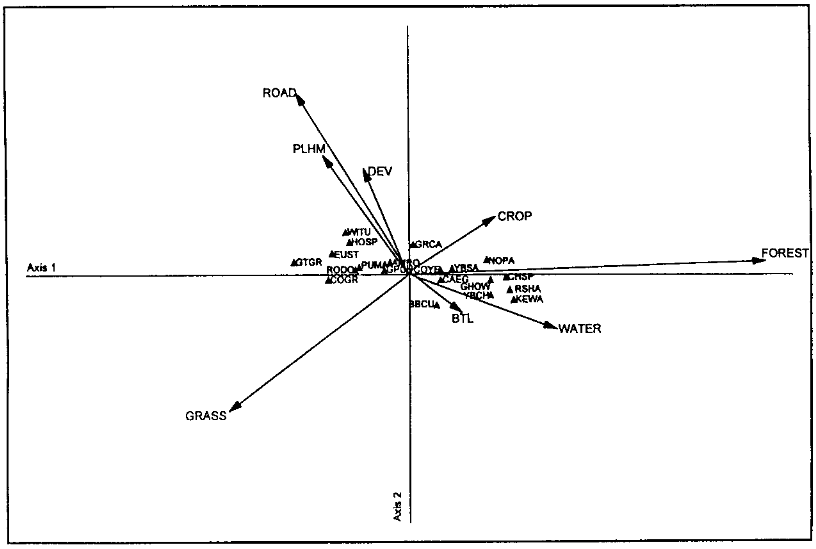

Fig. 4. Distribution of 20 species of birds in the high density rural population (intensively managed) landscape. Canonical correspondence analysis (CCA) ordination diagram with birds (▲) and environmental variables (vegetation cover types; arrows). The bird species are: BBCU = black-billed cucko, CAEG = cattle egret, YBCH = yellow-breasted chat, CHSP = chipping sparrow, COYE = common yellowthroat, GHOW = great-horned owl, GPCH = greater prairie chicken, KEWA = Kentucky warbler, NOPA = northern-parula warbler, RSHA = red-shouldered hawk, YBSA = yellow-bellied sapsucker, AMRO = American robin, GRCA = gray catbird, COGR = common grackle, GTGR = great-tailed grackle, HOSP = house sparrow, PUMA = purple martin, RODO = rock dove, EUST = European starling, and WITU = wild turkey. Environmental variables are: DEV = developed area, ROAD = road, WATER = water, CROP = cropland, PLHM = pasture land and hay meadows, GRASS = native grassland, FOREST = scrub forest, and BTL = brush-treated land.

Table 7. Canonical coefficients and intraset correlations for variables of the stepwise canonical correspondence analysis carried out on landscape cover type and structure in a low density rural population (extensively managed) and high density rural population (intensively managed) landscape.

	Canonical coefficients		Intraset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Low density rural population				
Vegetation covery types				
Developed area	0.1886	0.3512	0.3773	0.2696
Cropland	0.2381	0.5417	0.4600	0.5967
Pasture land/hay meadows	0.0137	0.0671	0.2043	0.3519
Native grassland	-0.3543	0.1984	-0.4498	0.3153
Scrub forest	0.4993	-0.4171	0.8592	-0.4816
Brush-treated land	-0.3345	0.0373	-0.4836	-0.1067
Roads	-0.0772	0.1264	-0.2431	0.2208
Water	0.1993	0.4134	0.2424	0.6642
Bare ground	-0.0204	0.0211	0.0368	-0.1659
Landscape structure				
Mean patch size	0.2962	-0.1888	0.6066	-0.3657
Fractal dimension	0.3953	0.3719	0.1616	0.5995
Richness	-0.6962	3.8510	-0.6140	0.5035
Shannon diversity	-0.9746	-4.4340	-0.5840	0.2190
Dominance	-1.2727	-4.0655	0.2108	0.0841
Contagion	1.3820	-0.4068	0.2636	0.4771
Angular second moment	-0.4582	1.0816	0.7338	0.2551
High density rural population				
Vegetation cover types				
Developed area	-0.0909	0.2804	-0.1122	0.4117
Cropland	-0.1380	0.2842	0.2237	0.2307
Pasture land/hay meadows	-0.4134	0.4857	-0.2183	0.4710
Native grassland	-0.6146	-0.0212	-0.4644	-0.5497
Scrub forest	0.5798	0.2718	0.9362	0.0521
Brush-treated land	0.0144	-0.0606	0.1327	-0.1508
Roads	-0.0822	0.6983	-0.2805	0.7025
Water	0.2035	0.0395	0.3795	-0.2206
Bare ground	-0.0030	-0.3156	0.0046	-0.2329
Landscape structure				
Mean patch size	0.5554	0.4059	0.8089	0.3836
Fractal dimension	-0.0703	-0.3182	-0.3795	-0.2690
Richness	-0.4051	2.1382	-0.4256	-0.4442
Shannon diversity	-0.1789	-0.6500	-0.7334	-0.1809
Dominance	0.0057	0.1669	0.6437	-0.1278
Contagion	0.8441	-2.8708	0.6586	-0.4575
Angular second moment	-0.4587	2.3910	0.7392	0.1250

determining avian community composition (Rotenberry 1985). However, Flather and Sauer (1996) concluded resident species showed few correlations with landscape structure in the eastern United States. In addition, most biodiversity studies focused on forests or woodland areas, but little research was conducted in the tallgrass prairie ecosystem. Our results support Roth (1976) and Wiens (1974) comments that generalizations relating vegetation structure and complexity to avian community composition were unrealistic for grasslands. While brush and forests vary broadly in vegetation structure and composition, which correlate with avian diversity, the degree of variability of heterogeneity among grasslands at the landscape scale is so subtle that its affect on avian diversity can be obscured (Knick and Rotenberry 1995). This may explain the inability of our landscape structure variables to explain temporal changes in avian community composition.

Conclusions and Management Implications

Changes in land use and vegetation cover types were related to changes in the avian community composition in this study. Avian communities in the high density rural population (intensively managed) and low density rural population (extensively managed) landscapes diverged over time because of different land use and management practices associated with each landscape. Temporal shifts in avian community composition were reflected in increases of some prairie species in the low density rural population and generalist associated species in the high density rural population landscapes. To preserve prairie birds and maintain biological diversity of prairie bird assemblages, management practices should increase the abundance and quality of native plant communities, especially grasslands. Maintenance of the tallgrass prairie by prescribed burning, judicious herbicide use for control of exotic and invasive plants, and grazing management are generally conducive to this objective. However, intensive land uses and management practices associated with areas surrounding urban centers pose a threat to the integrity of native plant communities. Although different variables explained avian community composition in the 2 landscapes, management practices that alter landscape structure may have less impact on avian community composition than changes in vegetation cover types.

Hence, biologists and conservationists in this region should focus attention on preserving biological diversity of rural ecosystems by maintaining native plant communities. In 1989, 74% of the United States population resided in urban areas, and that number is expected to increase to >80% by the year 2025 (Haub and Kent 1989). Considering the growth of metropolitan areas in the United States, knowledge of ecosystems under the influence of urbanization can only become increasingly important (McDonnell and Pickett 1990). In the absence of societal pressure to halt urban sprawl and agricultural intensification in rural landscapes, ecosystem integrity and bird communities may continue to degrade.

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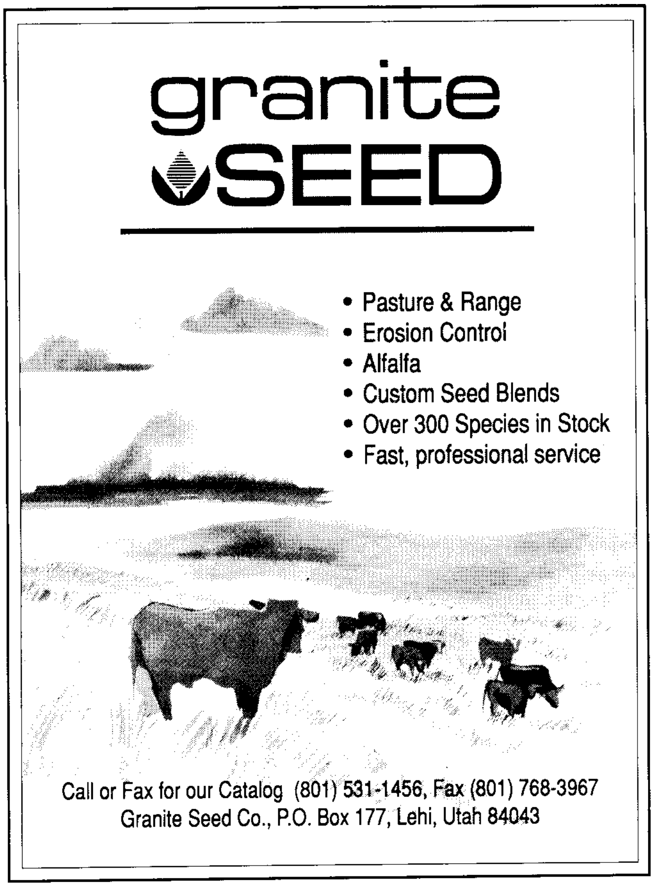

J. Range Manage.
52:431–435 September 1999

Goats locomotion energy expenditure under range grazing conditions: Seasonal variation

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Abstract

The estimation of the energy cost of various activities using calorimetric techniques in conjunction with direct field observations can be used to estimate energy expended in the daily activities of free-ranging animals. The objective of this study was to observe and quantify the grazing activities and to estimate the energy expenditure due to locomotion of goats in open range.

The study was carried out at 'Finca de Bonaya' privately-owned site, which extends over 1,482 ha, located in the Nevada mountain-range, Almería. The local altitude varies from 1,100 to 2,000 m above sea level. The area has a mediterranean mountain climate, with annual precipitation ranging from 400 to 700 mm and average daily temperatures from 4.7°C in winter to 23.0°C in summer. Landscape is characterised by holm-oak wood and pine wood, degradation scrubs and hydrophilic grasses communities.

The experimental flock grazed on 3 routes during the whole year. The goats were released to graze during the day and then returned to an enclosed shed. The type of goat management was considered as semi-extensive. Direct observation was used to simulate the total distance walked, the vertical ascent or descent, and to quantify other grazing activities. Data on activities on range and distance travelled were taken on 3 days in each season. The energy expenditure of locomotion was calculated from the horizontal and vertical components of travel and the corresponding costs, which had been previously obtained by calorimetry.

There was no significant seasonal effect on period devoted to specific activities on range ($P>0.05$). However, significant changes in the estimated daily energy expenditure and extra energy expenditure due to locomotion of the animals at pasture were found in different seasons ($P<0.05$). Grazing and walking were the primary activities of goats throughout the study, accounting for 51.7 and 42.0% of the animals' daily period on range, respectively. Daily travelled distances by goats on range fluctuated from 12,777 m in summer to 8,100 m in autumn, with an annual average of 9,954 m, which represents a mean speed of 20.8 m/min calculated over the whole period on range. The mean annual vertical ascent or descent was 500 m. Estimated heat production due to locomotion ranged from 130.9 to 88.5 kJ/kg$^{0.75}$ per day in summer and autumn respectively. These values account for an increased metabolizable energy (ME) requirement at pasture above maintenance of 46.6 and 31.6%, respectively, assuming a ME requirement for maintenance of 401 kJ/kg$^{0.75}$ per day for the restrained goat.

Key Words: goats, locomotion, grazing, heat production.

Resumen

El coste energetiéo de varias actividades, obtenido mediante técnicas calorimétricas, junto a observaciones directas, realizadas en campo, puede utilizarse para estimar la energía transformada en las actividades que realizan los animales en pastoreo. El objetivo de este trabajo fue observar y cuantificar las actividades diarias relacionadas con el pastoreo y estimar el gasto energético debido a la locomoción de cabras en producción extensiva.

El estudio se realizó en la "Finca de Bonaya", de propiedad particular, de 1,482 ha, situada en Sierra Nevada, en la provincia de Almería, con altitud que varía entre 1,100 y 2,000 m sobre el nivel del mar. Su clima es mediterráneo de montaña, con 400 a 700 mm de precipitación anual y temperatura media que oscila entre 4,7°C, en invierno, y 23,0°C, en verano. Contiene áreas de robledal y pinar, monte bajo y comunidades de gramíneas hidrofílicas.

A lo largo del año el rebaño experimental pastaba siguiendo 3 recorridos, accediendo al campo por la mañana y regresando a un redil protegido. El sistema de manejo se considera semi-extensivo. Se empleó la observación directa para calcular la distancia recorrida, las diferencias en altitud, en ascenso y descenso, y para cuantificar las distintas actividades de los animales en pastoreo. Tales datos se tomaron durante 3 días en cada estación del año. El gasto energético de la locomoción se calculó a partir de los componentes vertical y horizontal del desplazamiento efectuado y sus correspondientes costes energéticos, obtenidos previamente por calorimetría.

No se observaron diferencias significativas entre estaciones respecto al periodo relativo que los animales en pastoreo dedicaron a actividades específicas ($P>0,05$). Sin embargo, se observaron entre estaciones cambios significativos en gasto energético diario y en la cantidad de energía adicional debida a la locomoción ($P<0,05$). Las actividades relacionadas con la ingestión de pasto y la locomoción fueron las dos actividades más importantes observadas en este estudio, alcanzando el 51,7 y 42,0% del periodo diario de permanencia de las cabras en el campo, respectivamente. Las distancias que las cabras recorrían al día variaron entre 12.777 m en verano y 8.100 m en otoño, con un promedio anual de 9954 m, lo que representa una velocidad media de desplazamiento de 20.8 m/min si el cálculo se realiza sobre el tiempo total de permanencia en pastoreo. La diferencia de altitud media del recorrido fue de 500 m, tanto en ascenso como en descenso. La producción de calor debida a la locomoción se situó entre 130,9 y 88,5 KJ/Kg$^{0.75}$ y día, en verano y otoño, respectivamente. Estas cifras representan un aumento en necesidades de energía metabolizable (EM) para el mantenimiento de 46,6 y 31,6%, respectivamente, asumiendo un valor de 401 KJ EM/Kg$^{0.75}$ y día para las necesidades de mantenimiento del animal en estabulación.

This work was supported by LUCDEME Program (CSIC-ICONA).
Manuscript accepted 13 Dec. 1998.

Goats are well adapted to the hot and dry conditions of the semi-arid areas of southern Spain, where they are widely reputed to give rise to a great productivity (Boza and Sanz Sampelayo 1997). Goats are able to harvest an adequate diet even when forage is scarce and they can graze over rugged and otherwise inaccessible terrain (Lu 1988). In arid lands, goats have to travel long distances for adequate food and water, and thus, their energy expenditure increase outstandingly. The extra energy expenditure related to physical activity of the grazing animal may affect its productive performance and may be influenced by seasonal variation in grazing activities (Lachica et al. 1997a).

The energy requirements for maintenance of grazing ruminants has been reported to be from 0 to 100% greater than those found for animals in confinement, with the cost of travel contributing substantially to this increase (see Lachica et al. 1997a).

The energy cost of various activities estimated using calorimetric techniques can be used in conjunction with direct field observations to estimate daily energy expenditure of free-ranging animals with advantages over other methodologies developed to measure or estimate the energy expenditure of unrestrained animals (Osuji 1974, Prieto et al. 1992), due to uncertainties about the reliability of these available techniques. The usual procedure for measuring the total energy expenditure by grazing animals is a factorial method, whereby the increase in energy expenditure above that measured in confinement is quantitatively estimated from calorimetric determination of the energy cost of various activities. The energy cost of each activity is then multiplied by the total time spent by free-ranging animals performing that activity and total extra energy expended is calculated by summation. Data on energy requirements of confined goats for maintenance and milk production have been obtained from calorimetric measurements in our laboratory (Aguilera et al. 1990, Prieto et al. 1990). Also, the energy cost of locomotion has been determined (Lachica et al. 1997b). This joined information allows to obtain accurate estimations of daily energy expenditure of goats on free range conditions. The described procedure is more advisable than extrapolation of theoretical allowances (i.e. NRC 1981) due to variations in grazing activities induced by environmental effects, as reported earlier (Lachica et al. 1997a).

The present work was designed to obtain additional information on the evaluation of seasonal effects on grazing activities of goats in the Mediterranean ecosystems of southern Spain and on changes they may cause in their daily energy expenditure.

Study Area

The study was conducted on a 1,482-ha privately-owned area called ‘Finca de Bonaya’, located in the Nevada mountain-range, between Laujar de Andarax and Paterna del Río, in the province of Almería, in southern Spain (latitude 37° 02.9' N and longitude 2°54.8' W). The topography is rugged, varying in elevation from 1,100 to 2,000 m above sea level. The climate in this region is typified as mediterranean mountain with rainfall variation of 400 and 700 mm. Summer is characteristically dry. The order of maximum precipitation is winter, autumn, spring, and summer. The average seasonal temperatures range from 4.7°C in winter to 19.4°C in summer.

This area was chosen to carry out the present study because of being rather similar to one used for a previous study (Lachica et al. 1997a) as far as their topographic and climatic characteristics is concerned, but there were important differences in vegetation communities. This later factor was assumed to have an important effect on grazing activities and behaviour of the animals. In this private area a representative flock of goats was available.

The vegetation of the area is dominated by trees formations: holm-oak (*Quercus rotundifolia Lam.*) and pine (*Pinus silvestris L. and P. Nigra Arnold*), degradation scrubs and hydrophilic grasses communities. The most abundant plant species of interest for goat production are listed in Table 1 in decreasing order of palatability. A catalogue of the vegetation of the area has been published by Fernández (1995). This author’s article also reports on the evaluation made of total phytomass (9,931 kg/ha) and forage phytomass (1,718 kg/ha) of the area.

Materials and Methods

The experimental flock was composed of 350 heads (17 males and 333 lactating females). The goats were of the "Malagueña" and "Serrana" breeds and

Table 1. Plant species of interest for goat production in ‘Finca de Bonaya’ (southern Spain).

[1]*Adenocarpus decorticans Boiss*
[2]*Dactylis glomerata L.*
[2]*Koeleria crassipes Lange*
[1]*Quercus rotundifolia Lam.*
[1]*Crataegus monogyna Jacq.*
[1]*Fumana ericoides (Cav.) Gand.*
[1]*Helianthemum apenninum (L.) Miller*
[1]*Helianthemum cinereum (Cav.) Pers..*
[2]*Argyrolobium zanoni (Turra) P.W. Ball*
[2]*Euphorbia flavicoma DC.*
[2]*Hieracium pilosella L.*
[1]*Rhamnus myrtifolius Willk.*
[1]*Dorycnium pentaphyllum Scop.*
[2]*Ononis repens L.*
[1]*Prunus ramburii Boiss.*
[1]*Rosa canina L.*
[2]*Anthyllis vulneraria L.*
[2]*Avenula bromoides (Gouan) H. Scholz*
[1]*Genista cinerea DC.*
[1]*Cistus clusii L.*
[1]*Cytisus oromediterraneus Boiss*
[1]*Genista umbellata Poir.*
[1]*Lavandula stoechas DC.*
[2]*Sanguisorba minor Scop.*
[1]*Staehelina dubia L.*
[2]*Corynephorus canescens (L.) Beauv.*
[2]*Carlina corymbosa L.*
[2]*Eryngium campestre L.*
[2]*Teucrium compactum Clemente ex Lag.*
[1]*Ulex parviflorus Pourret*
[1]*Artemisia campestris L.*
[1]*Cistus albidus L.*
[2]*Festuca lemanii*
[2]*Festuca trichophylla (Ducros ex Gaudin) K. Richter*
[1]*Genista scorpius (L.) DC.*
[1]*Genista versicolor Boiss.*
[1]*Thymus serpylloides Bory*
[2]*Festuca elegans Boiss.*
[1]*Bupleurum spinosum L.*
[1]*Erinacea anthyllis Link*
[1]*Helichrysum stoechas (L.) Moench*
[2]*Nardus stricta L.*
[1]*Santolina chamaecyparissus L.*
[1]*Teucrium polium L.*
[1]*Thymus zygis L.*
[2]*Andryala integrifolia L.*
[2]*Arrhenatherum elatius (boiss. & Reuter) Romero Zarco*
[1]*Berberis hispanica Boiss. & Reuter*
[2]*Brachypodium retusum (Pers.) Beauv.*
[2]*Festuca indigesta Boiss.*
[2]*Festuca scariosa (Lag.) Ascherson & Graebner*
[1]*Lavandula lanata Boiss.*
[2]*Melica minuta L.*

[1] Woody plants.
[2] Herbaceous plants.

their respective cross-breeds. After morning milking, the goats grazed during the day under the supervision of a shepherd and then returned to an enclosed shed, in which they spent the night. The type of goat management is considered as semi-extensive, for commercial milk production (annual yield 280 liters/animal on average) and meat (carcasses of young kids mainly).

Three routes which were usually followed by the herd, identified as route 1, 2, and 3, were used in this study. They were at 1,600–2,000 m, 1,500–2,000 m and 1,000-1,600 m above sea level, respectively.

A direct observation procedure, described by Somlo et al. (1991a) and Lachica et al. (1997a), was used to quantify time spent on each activity on the range and also to measure total distance walked, vertical ascent or descent. Briefly, the track of a randomly selected lactating female was followed for 10 minutes on foot by 2 observers, one for annotating the animal's grazing activities and another for quantification of the distance travelled. During this 10-minute period this single animal was assumed to be a reliable indicator of the flock activity. At the end of the observation period the nearest goat was followed in a similar way. The procedure was repeated 28 ± 6 times during the day throughout 3 consecutive days (each day, a different route was studied) during each of 4 seasons. The method allows a number of animals to be monitored with minimal labour. In an earlier work (Lachica et al. 1997a) no differences ($P > 0.05$) were found between data of locomotion activities taken simultaneously by 2 observers from different goats of a single herd. For that reason only 1 observer was employed in this trial. Activities were divided into several major categories: grazing, defined as the time spent searching for and ingesting forage; walking, defined as the movement from one place to another without grazing; standing, defined as no activity; ruminating, defined as the time spent to rumination; and others (socialising, etc.).

For locomotion studies, the observer carried 1 pedometer and 1 altimeter. The pedometer (Podomatic, Eschenbach Optic, Nuremberg, Germany) was attached vertically to the observer's belt. The distance travelled was recorded on a digital indicator and subdivided from 25 m up to 100 km. A stride indicator allows adjustment of the instrument to the step length of the bearer. Several tests of the accuracy of the pedometers were conducted at the beginning of each trial. The corresponding calibration factors of the instruments were obtained by dividing a known distance walked by the pedometer reading. These values were employed to convert pedometer readings into actual distances walked. Somlo et al. (1991b) concluded that pedometers are inaccurate when carried by goats. The average pedometer calibration factors (distance travelled/distance recorded) and their coefficients of variation indicate the reliability of the records made in the present work (mean value 1.087 ± 0.0248; CV = 7.23%; n = 10) The altimeter employed to determine the vertical ascent or descent (Altiplus N1, Pretel, France) is an electronic instrument with several functions (altitude, altitude variation, temperature, barometric pressure). Altitude is calculated from atmospheric pressure with a resolution of 1 meter and ranges from –256 to 9,999 m. Temperature readings are in the range of –25°C to 55°C, with an accuracy of about 1°C.

Daily energy expenditure due to locomotion was calculated from both the horizontal and vertical (ascent and descent) components of goat's travel (obtained by means of pedometer and altimeter readings) and the corresponding energy cost (3.35 and 31.7 J/kg^{-1} × m^{-1} for horizontal travel and vertical ascent, respectively) and energy recovery (–13.2 J/kg^{-1} × m^{-1} for vertical descent), which had been obtained by calorimetry trials using a confinement respiration chamber (Lachica et al. 1997b). The results were extrapolated to total time spent by the goats on range during each of 4 seasons and expressed in terms of animals of average liveweight. For example, a 38 kg goat travelling an horizontal distance of H m, ascending A m and descending D m in the course of 24 hours would expend $38 \times (H \times 3.35 + A \times 31.7 - D \times 13.2)$ J. The energy expenditure obtained by this calculation was then compared with the energy requirements for maintenance of the goat, which had been previously determined by open-circuit calorimetry (401 kJ/kg$^{0.75}$ per day; Aguilera et al. 1990). From these data the increased energy requirements above maintenance due to activity of grazing goats were calculated.

Seasonal effects on locomotion activities were analysed from data taken by the observer throughout the 3 consecutive days within each season by means of a one-way analysis of variance, where season was used as error. Tukey's test was used to determine significant differences ($P<0.05$) among means.

Results and Discussion

Grazing and walking were the primary activities of goats throughout the period of study (values of activities in summer are missing), accounting for, on average, 51.7 and 42.0% of the animal-day period, respectively (Table 2). Time spent on these activities, as percentage of daily period on range, was not significantly affected by season ($P > 0.05$).

The distance travelled daily by the goats on range (Table 3) was significantly affected by season ($P < 0.05$) and fluctuated from 12,777 m in summer to 8,100 m in autumn, with an annual average of 9,954 m. This value was calculated over the whole period on range, not over the time spent walking, and represents a mean annual daily speed of 20.8 m/min. The average speed of travel, estimated overtime on locomotion, was 49.1 m/min, somewhat higher than the animal mean value which can be calcu-

Table 2. Seasonal changes in daily activities (%) of goats on range. (Values are means of 3 days of observation)

	Grazing	Walking	Standing	Ruminating	Others
			(%)		
Autumn	49.9	41.1	6.7	1.5	0.8
Winter	52.3	42.4	2.9	2.0	0.4
Spring	52.9	42.6	3.9	—	0.6
Summer	—	—	—	—	—
$x \pm \sigma/\sqrt{n}$	51.7±0.75	42.0±0.38	4.5±0.93	1.8±0.18	0.6±0.09
Seasonal effect[1]	NS	NS	NS	—	—

[1] NS, not significant ($P>0.05$).

Table 3. Mean distance travelled daily by goats at pasture. (Values are means of 3 consecutive days)$

	Time spent at pasture	Distance travelled	Vertical ascent or descent	Mean speed	Mean speed
	(h)	(m)	(m)	(m/min)[1]	(m/min)[2]
Autumn	7.2^{a}	8100^{a}	500	18.7^{a}	45.6
Winter	6.4^{a}	9003^{ab}	500	23.7^{a}	55.3
Spring	8.4^{b}	9935^{ab}	500	19.7^{a}	46.3
Summer	10.0^{c}	12777^{b}	500	21.3^{a}	—
Annual mean	8.0	9954	500	20.8	49.1
Pooled std. error	0.12	680.5	28.9	1.51	
Range	(5.7–10.0)	(6090–15192)	(400–600)	(15.2–30.1)	
Seasonal effect[3]	*	*	—	—	—

$Within the same column values bearing different superscripts are significantly different ($P<0.05$).

[1] Calculated over the whole daily period on range.

[2] Calculated over the time spent walking.

[3] * $P<0.05$

lated from data previously published (41.5 m/min; Lachica et al. 1997a). The mean annual vertical ascent or descent was 500 m. It is widely accepted that goat's grazing behaviour and diet selection are markedly influenced by seasonal availability of forage. Some information at this respect from dry areas of southern Spain has been obtained in our laboratory (Somlo et al. 1991a, García et al. 1994, Molina Alcaide et al. 1997). The availability of forage may be the main factor affecting physical activity of freely ranging animals and therefore their extra energy expenditure. In our study the estimated heat production due to locomotion increased steadily from autumn to summer (Table 4). Seasonal effect was significant ($P<0.05$). Extreme values were 88.5 and 130.9 kJ/kg$^{0.75}$ per day with an annual mean value of 105.6 kJ/kg$^{0.75}$ per day. Assuming a metabolisable energy (ME) requirement for maintenance of 401 kJ/kg$^{0.75}$ per day (Aguilera et al. 1990) and a net efficiency of utilization of ME for maintenance (k_m) of 0.70, these increases in heat production account for an extra ME requirement above that of maintenance in the range of 46.6 and 31.6% for summer and autumn periods, respectively ($P < 0.05$), corresponding to a mean extra energy expenditure of 37.6%. This average value is higher than the mean increase of 11.0, 25.4 and 32.1% estimated for free ranging sheep by Blaxter (1967), Langlands et al. (1963) and Osuji (1974), respectively, but is markedly lower than values reported for free ranging cattle (53.8% (Reid 1958), 74.4% (Wallace 1955), 52.2–106.7% Hutton (1962)) and sheep (49.2% (Lambourne and Reardon 1963), 60.0–70.0% (Young and Corbett 1972), 62.7–91.5% (Coop and Hill 1962)). The National Research Council (NRC 1981) has a tabulated mean value of 424 kJ ME/kg$^{0.75}$ for the maintenance requirements of the goat and makes an extra allowance of energy to be added to account for the increased muscular activity of the animals under grazing conditions: a 25% increment in case of light activity; a 50% increment on semiarid rangelands and on slightly hilly lands; and a 75% increment for long-distance travel on sparsely vegetated grasslands or on mountainous transhumance pastures. The application of these tabulated values to our experimental conditions would overestimate the animals energy expenditure due to locomotion. Moreover, the average value for the increase in energy expenditure over maintenance found in this work is 2.4 times higher than that obtained in a previous study carried out in another semiarid zone of the same geographic area (Lachica et al. 1997a). This fact indicates that it is inappropriate to extrapolate theoretical allowances for activity even to apparently similar conditions. A direct estimation of the time spent on different activities on range, and particularly the distance travelled, will aid for an accurate estimation of the extra expenditure of energy under grazing conditions, as performed in this work.

Table 4. The energy cost of locomotion of goats at pasture during the different seasons of the year. (Values are means of 3 consecutive days)[1]

	Live weight	Heat production (HP)	Estimated increased in ME requirements over maintenance[2]
	(kg)	(kJ/kg$^{0.75}$)	(%)
Autumn	35	88.5^{a}	31.5^{a}
Winter	35	95.9^{ab}	34.2^{ab}
Spring	40	107.0^{ab}	38.1^{ab}
Summer	40	130.9^{b}	46.6^{b}
Annual mean	37.5	105.6	37.6
Pooled std. error	0.0	4.65	1.66
Seasonal effect[3]		*	*

[1] Within the same column values bearing different superscripts are significantly different ($P<0.05$).

[2] MEm=401 kJ/kg$^{0.75}$ per day (Aguilera et al., 1990); Km=0.70.

[3] * $P<0.05$

Conclusions

The method employed appears to be adequate to simulate and quantify grazing activities of goats on open range by means of direct observation. It is simple and easy to apply to field conditions, requiring only 1 observer for locomotion studies. The results also showed that the energy cost of locomotion represented a substantial contribution to the energy expenditure of goats on range. This study will facilitate a more accurate estimation of the energy requirements on range and will contribute to define the stocking rate in the area under study.

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J. Range Manage.
52:436–439 September 1999

Conditioned aversion to minimize *Ferula communis* intake by orphaned lambs

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Abstract

The circum-Mediterranean perennial *Ferula communis* L. (giant fennel) has anticoagulant constituents. Mortality from poisoning can affect 5% of the sheep grazed in infested areas and most casualties are ewe-lambs at the onset of the grazing season. In intensive sheep production systems, ewe-lambs are “orphaned”, artificially reared, and have no opportunity to acquire safe dietary habits by imitating their mothers. The aim of the present study was to evaluate the intake of *F. communis* in such lambs and to assess the potential of using conditioned aversion as a managerial tool to decrease the frequency of *F. communis* poisoning. Six lambs weighing approximately 28 kg were averted to *F. communis* using 2 administrations of 4g LiCl in aqueous solution, given immediately after a meal of *F. communis*; 6 similar lambs served as unaverted controls. The intake of *F. communis* and the persistence of aversion were assessed over 7 observation days using a simulation of an infested field where freshly cut bunches of *F. communis* were tied to stakes at 10-m intervals in ryegrass *(Lolium multiflorum* Lam.) paddocks at the late vegetative stage. Averted lambs grazed separately from unaverted counterparts. Time spent by lambs foraging on *F. communis* was in the range of 0–0.015 min/hour (not significantly different from nil) in averted, and 0.15–0.24 min/hour in unaverted lambs, respectively (P = 0.002). Consequently, the rate of disappearance of *F. communis* was greater when grazing was by unaverted than averted lambs (0.29 and 0.15 g/min, P = 0.01). The aversion persisted for 25 days after the LiCl treatment, at which time observations were discontinued. Assuming that the amount of *F. communis* that disappeared is close to actual intake by lambs, intake by unaverted lambs was high enough to endanger the lambs, whereas averted lambs consumed safe amounts of the poisonous plant. It is concluded that conditioned aversion has the potential to alleviate the problem of *F. communis* poisoning in orphaned ewe-lambs.

Key Words: Sheep grazing; poisonous plants; conditioned food aversion

Resumen

La especie perenne circunmediterranea *Ferula communis* L. ("Giant fennel") tiene constituyentes anticoagulantes. La mortalidad por envenenamiento con esta especie puede afectar hasta el 5% de los borregos apacentando áreas infestadas, la mayoría de las bajas son corderos hembras y ocurren al final de la estación de apacentamiento. En sistemas de producción intensiva de ovinos, los corderos hembras son destetadas y alimentados artificialmente por lo que no tienen la oportunidad de adquirir hábitos de alimentación segura a través de imitar a sus madres. El objetivo de este estudio fue evaluar el consumo de *F. communis* en corderos destetados y el potencial de uso de la aversión condicionada como una herramienta de manejo para disminuir la frecuencia de envenenamiento con *F. communis.* Seis corderos de aproximadamente 28 kg de peso fueron condicionados adversamente a *F. communis* mediante 2 administraciones de 4 g de LiCl en solución acuosa suministrada inmediatamente después de una comida de *F. communis*, seis corderos similares sin aversión fueron utilizados como control. El consumo de *F. communis* y la persistencia de la aversión a esta especie fueron evaluados durante 7 días mediante la simulación de un terreno infestado. La simulación se realizó en una pradera de ryegrass (*Lolium multiflorum* Lam.) donde manojos recién cortados de *F. communis* se ataron a estacas con una separación de 10 m, la pradera estaba a finales de la etapa vegetativa. Los corderos con aversión apacentaron separadamente de los corderos sin aversión. El tiempo utilizado en apacentar *F. communis* estuvo en el rango de 0 a 0.015 min/ hr (Sin diferencia significativa de nil) para los corderos con aversión y de 0.15 a 0.24 min/ hr para los corderos sin aversión (P = 0.002). Consecuentemente, la tasa de desaparición de *F. communis* fue mayor con el apacentamiento de corderos sin aversión que con aversión (0.29 y 0.15 g/min, P = 0.01). La aversión persistió por 25 días después del tratamiento con LiCL, tiempo en que se suspendió la observación de los animales. Asumiendo que la cantidad de *F. communis* que desapareció es cercana al consumo actual por los corderos, el consumo de los corderos sin aversión fue suficientemente alto para ponerlos en peligro, mientras que los corderos con aversión consumieron cantidades de esta planta tóxica que no fueron peligrosas. Se concluye que la aversión condicionada tiene potencial para disminuir el problema de envenenamiento de corderos hembra por *F. communis.*

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We thank Dr. Menahem Zachs and the Jewish National Fund for partial funding of this project. Contribution from the Agricultural Research Organization, Institute of Field and Garden Crops, Bet Dagan, Israel, No. 114/98.

Manuscript accepted 8 Nov. 1998.

The circum-Mediterranean perennial *Ferula communis* L. (giant fennel) is known to contain anticoagulant constituents in healthy, fresh plant material (Shlosberg and Egyed 1985). Mortality can affect 5% of the sheep grazed on infested areas. Most casualties are ewe-lambs at the onset of the grazing season within 30 days of being turned out, probably because at that time *F. communis* is prominent and lush whereas alternative herbaceous vegetation is still scarce (Egber et al., unpublished data). In the intensive lamb meat production system practised in Israel, ewe-lambs are separated from their mothers at birth (i.e., "orphaned"), raised artificially using an automatic milk dispenser, and weaned to solid food at 25–30 days of age and 12–15 kg body weight (BW). While learning from adults is considered of major importance in acquiring safe dietary habits (Thorallsdotir et al. 1990, Provenza et al. 1993), there is little opportunity for adults to influence the dietary habits of young animals in this type of production system. Also, autumn-born lambs can be first turned to green pasture when 3-months old but do not interact socially with adult ewes during the first grazing season (Egber unpublished data). Herbicidal eradication of *F. communis* was practised in the past, but it is now considered ecologically unsound. In regions where *F. communis* is widespread, shepherds will defer grazing and alternate grazing in infested and non-infested paddocks to prevent poisoning, which results in incomplete exploitation of pasture (Shlosberg and Egyed 1985). While *F. communis* is toxic when fed to lambs at 2.5 g/kg BW/day, it causes no disturbance in blood clotting at 1.0 g/kg BW/day (Shlosberg and Egyed 1985). Toxicity of *F. communis* decreases somewhat after the plant has flowered (Egyed et al. 1981). There is no quantitative information available on *F. communis* intake by weaned lambs grazed on infested range.

It appears that no post-ingestive discomfort is felt when sheep feed on *F. communis* (Shlosberg and Egyed 1985) and the plant is abundant and palatable. These are favorable conditions for the implementation of conditioned food aversion (CFA) against *F. communis*, e.g. artificial build-up of temporal contiguity between ingestion of the plant and artificially induced post-ingestive pain, in order to elicit rejection by lambs at later encounters (Ralphs 1992). Lithium chloride (LiCl) has been used frequently as a malaise-inducing agent to establish a CFA procedure, due to its relative safety and taste analogy with sodium chloride (du Toit et al. 1991). The procedure has been shown to induce persistent CFA to *Cercocarpus montanus* and *Amelanchier alnifolia* in sheep by Burritt and Provenza (1989), to *Oxytropis sericea* (Ralphs et al. 1997) and *Delphinium barbeyi* (Ralphs 1997) in cattle, and to *Pinus brutia* in goat kids (Nolan and Nastis 1996). Procedures for conditioned food aversion (CFA) have been implemented in lambs accompanying their mothers (Provenza et al. 1993), in 3-month old weaned lambs (Burritt and Provenza 1990, du Toit et al. 1991) and in adult sheep (Provenza et al. 1993). We recently developed a procedure to establish CFA to *F. communis* in orphaned weaned lambs in individual cages. While testing the procedure in the field, we found that the efficacy of CFA to *F. communis* interacts with pasture availability (Egber et al., unpublished data). Others have shown that social facilitation causes sheep to extinguish aversions (Burritt and Provenza 1989, Provenza and Burritt 1991, Provenza et al. 1993). Therefore, the assessment of the efficacy of CFA and, in particular, the evaluation of its persistence, must be carried out under strictly controlled field conditions, where averted and non-averted lambs graze separately in similar plots, before any extrapolation to commercial range conditions.

This study was aimed at: (i) quantifying the intake of *F. communis* by weaned lambs at the onset of their first grazing season; and (ii) assessing the value of creating conditioned food aversion to *F. communis* as a potential aid to improve range utilization by sheep in infested regions under controlled field conditions.

Materials and Methods

The experiments were carried out at Kibbutz Har'el in the Judean Hills of Israel (31.7°N, 35.0°E), where rangelands are heavily infested with *F. communis*. Twelve weaned "orphaned" German Landschaff Merino ewe-lambs, aged 80 days and weighing approximately 27.8 kg (SE=0.90), were housed in individual cages (1.7 × 1.7 m) on a dirt floor in a roofed building. Six lambs served as averted group and 6 lambs served as controls. During the 2 weeks before attempting to establish aversions to *F. communis* was implemented, lambs were fed daily a basic diet comprising 300 g of a commercial starter concentrate (18% crude protein, Ambar, Hadera, Israel) and 300 g of chopped oat hay containing 8.1% crude protein (CP), 68.5% neutral detergent fiber (NDF) and 42.1% acid detergent fiber (ADF) on a dry matter (DM) basis. Fresh water was available ad lib. As lambs were reluctant to consume *F. communis* foliage when it was offered in the trough, the plant was tied in bunches of approximately 200 g which were positioned vertically to the cage frames with metal clamps, so as to simulate the natural position of plants, as described by Meuret (1988) and Provenza et al. (1993). On March 27, when the average daily intake of *F. communis* foliage reached approximately 40 g (SE=9 g) fresh, a conditioned food aversion (CFA) protocol was carried out by administering 4 g LiCl in aqueous solution, immediately after *F. communis* was provided, independent of *F. communis* intake, using a de-worming gun (day 0). Sodium chloride was administered to the control lambs. No *F. communis* was provided on March 28. On March 29, *F. communis* foliage was presented to lambs, followed by a second administration of 4 g LiCl. Following the second LiCl administration, individual cages were dismantled, lambs were managed as 1 flock and turned to a late vegetative Italian ryegrass (Lolium multiflorum Lam.) paddock of 0.30 ha which had been sown in November and grazed occasionally from the beginning of January. It was divided into 2 similar plots, each of 0.15 ha. Lambs were accustomed to grazing in both plots as 1 group from day 4 to day 7 after the first LiCl treatment. Provision of the basic diet of oat hay was discontinued in order to enhance intake at pasture. Standing biomass and pasture quality were estimated by clipping five, 0.25 × 0.25 m quadrats in each plot. Samples were dried in a forced air oven at 60°C for 48 hours and then weighed. Initial standing biomass averaged 4,740 (SE=320) and 6,040 (SE=350) kg/ha in plots A and B, respectively; CP, ADF, NDF and ash content were similar in both plots and averaged 10.8%, 30.3%, 51.2% and 13.3%, respectively. The standing biomass throughout the experiment was similar in the two fields (Fig. 1).

An artificial simulation of a pasture infested with *F. communis* was constructed as follows: Nine, 1-m-high iron stakes were sunk 30 cm into the ground and their position was defined using a letter and a number. The distance between stakes was approximately 10 m, which is approximately the distance between *F. communis* plants in infested range. The lambs were grazed alternately on the 2 plots; averted and non-averted lambs grazed separately, and allocation of plots was switched every day. Grazing behavior on the *F. communis*-infested paddock was observed on 7 occasions from 4 April to 22 April. On these days, freshly cut bunches of *F. communis* weighing approximately 350 g fresh were tied tightly to the base of each stake, to mimic the natural appearance of the plant. Three bunches were weighed and laid out of lambs' reach for evaluation of water loss. Grazing bouts lasted 180 min., apart from 1 bout of 120 min. on 1 very hot day. At the end of each grazing bout the *F. communis* bunches were gathered, weighed and weight change was corrected for water loss. If uneaten residues of *F. communis* were found on the ground near stakes, their weight was subtracted from the initial weight of a bunch before disappearance of *F. communis* was calculated. Lambs were identified by numbers painted on both sides of the body. Two observers were allocated to each plot, and observations were made from a distance of 2 to 5 m. The presence of observers had no detectable effect on the grazing activity and social relationships of these "orphaned" lambs, because they were accustomed to being handled from birth. Every encounter of a lamb with *F. communis* was documented. When an animal started to forage on *F. communis* (an event we term a "grazing encounter"), the observer recorded the lamb number and the exact time. At the end of an encounter, the time was recorded again. Persistence of conditioned food aversion (CFA) was tested until day 25 after establishment of the CFA. On that date *F. communis* began to flower, and *F. communis* is attractive and toxic mainly before flowering (Egyed et al. 1981).

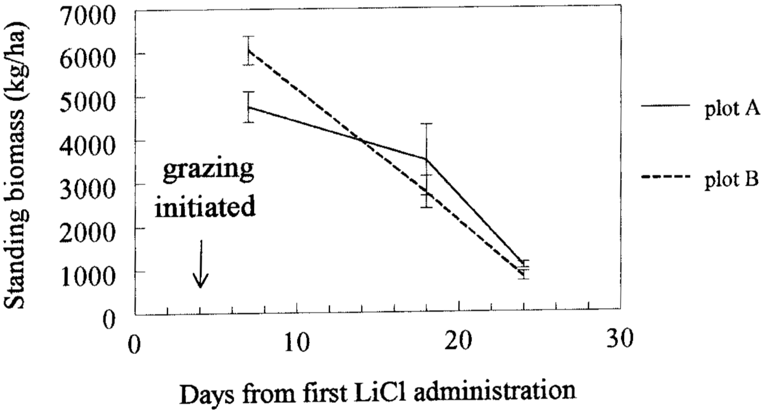

Fig. 1. Standing biomass (kg /ha) of plots A and B throughout the experiment.

The effects of the aversion procedure on the intake of *F. communis* were evaluated by analyses of variance using a repeated measures procedure with lamb-within- treatment as the error term (SAS 1985). The weight change of *F. communis* bunches was analyzed using a bi-factorial procedure with CFA (yes/no) and plot (A/B) as main effects and their interaction. The effect of the position of the bunch on the number of encounters and the intake of *F. communis* was analyzed separately for each plot, using a bi-factorial procedure with CFA (yes/no) and position of bunch as main effects and their interaction.

Results and Discussion

No difference (P=0.15, Fig. 2a) was noted in the frequency of grazing encounters to *F. communis* in lambs averted or not averted to the plant but significant "plot" (P=0.01) and "lamb" (P=0.03) effects were noted for the frequency of grazing encounters (P=0.01): some lambs grazed *F. communis* more frequently than others and plot B had 50% more grazing encounters to *F. communis* than plot A. The average time spent by a lamb foraging on *F. communis* ranged from 0 to 0.015 min/hour (not significantly different from nil) in averted, and 0.15–0.24 min/hour in unaverted lambs, more than 10-fold higher in the latter (P=0.002, Fig. 2b). A strong (P=0.008) "lamb" effect on time spent foraging on *F. communis* was found, implying that some lambs consumed much more *F. communis* than others. This finding is in agreement with the description by Shlosberg and Egyed (1985) of lambs that "were assertively aggressive in their desire to receive their daily portion".

Overall, no plot effect were observed for time spent foraging on *F. communis* (P=0.32), but a stake × aversion treatment interaction tended to be significant in plot B (P=0.06).

The aversion to *F. communis*, when assessed according to time spent foraging on *F. communis*, seemed to persist throughout the experiment (Fig. 2b). The location of *F. communis* bunches did not affect the frequency of visits and time spent foraging on them in plot A.

The rate of disappearance of *F. communis* was 0.218 g fresh/min/lamb. It was approximately double when grazed by non-averted, compared with averted, lambs (0.29 and 0.15 g/min, P=0.01). When disappearance was analyzed in a model which included aversion, plot, plot x aversion and date, the effect of aversion was significant (P=0.008) and aversion x plot tended to be significant (P=0.10). Rate of disappearance tended to be affected by stake position in plot B: 0.19 g/min for stakes A1-A2-A3, located along the fence between the 2 plots, compared with 0.13 g/min from other stakes (P=0.07); a similar trend was found in plot A: 0.17 g/min for stakes C1-C2-C3, also located along the fence between the 2 plots, compared with 0.12 g/min for other stakes (P=0.19). This finding can be interpreted as an outcome of lambs in the experimental groups to grazing as close as possible to mates of the other group. This strengthens our assumption that conditioned food aversion (CFA) had to be evaluated first with groups which were separated while grazing, because of the negative anticipated effects of unaverted controls on averted lambs

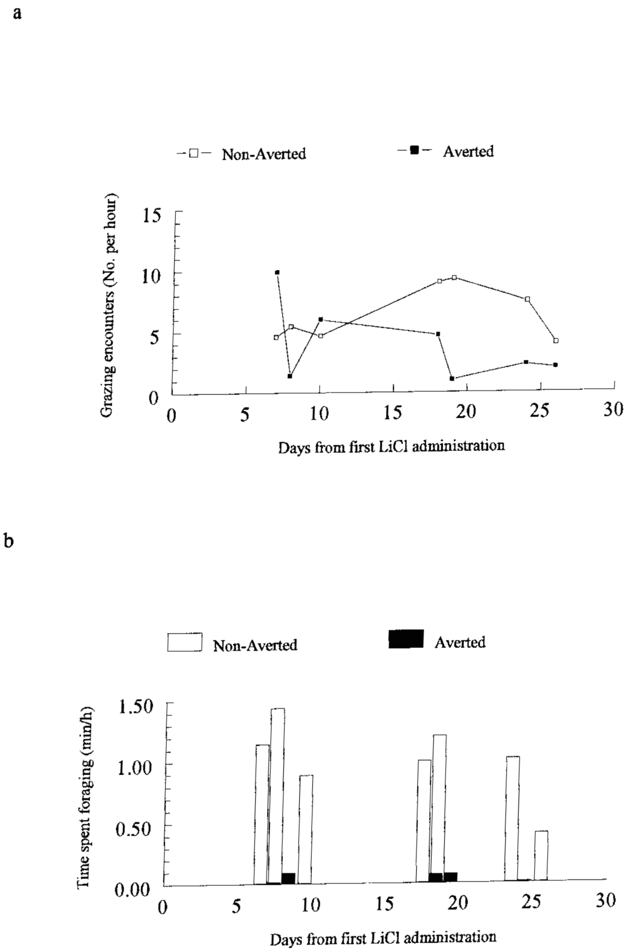

Fig. 2. The frequency of grazing encounters (a, lines) and time spent foraging (b, bars) on *F. communis* by lambs averted or non-averted to *F. communis*.

(Burritt and Provenza 1989; Provenza and Burritt 1991).

The rate of *F. communis* disappearance (0.218 g/min/lamb) was comparable to the 1.0 g/min found with 6 lambs in a previous trial (Egber et al., unpublished data). Assuming that most of the *F. communis* which disappeared was eventually eaten, it can be calculated that unaverted lambs consumed 17 g/hour, or approximately 70 g during a 4 hour grazing day. Although lambs spent only about 1 min/hour foraging on *F. communis*, the amount of *F. communis* presumably eaten was close to 2.5 g/kg BW/day. Supposing lambs were continuously grazing the infested paddock, which was not the case in the present study, this amount would be enough to impair prothrombin time in lambs within 9 days, and to be lethal within 11 days (Shlosberg and Egyed 1985). In contrast, the amount of *F. communis* consumed by the averted lambs (35 g/day) was approximately 1g/kg BW/day, an amount which did not produce noticeable toxic effects within 21 days, according to Shlosberg and Egyed (1985). Therefore, implementation of conditioned food aversion (CFA) to *F. communis* can be a viable management technique for ewe-lamb survival in *F. communis*-infested rangelands.

In addition, CFA to *F. communis* persisted for at least 25 days, which is approximately the period by which *F. communis* precedes the growth of most annual herbaceous plants. Therefore, CFA established in this critical period could alleviate the problem of *F. communis* poisoning in ewe-lambs. Poisoning in adult sheep is rare, however, visits to *F. communis* are common, which may negatively affect the grazing behavior of newly averted lambs. Therefore, the potential social influence must be studied before the procedure can be used on a wide scale, to determine whether only young ewe-lambs, or the whole flock, should be subjected to the CFA procedure and whether the CFA procedure should be repeated every year. The number of animals to be averted and the necessary frequency of the procedure for each animal are issues that will strongly affect the economic viability of this management option impact because the CFA procedure is difficult and time-consuming.

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Drought and grazing: I. Effects on quantity of forage produced

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Abstract

This research addresses the hypothesis that grazing intensity during and following drought can dramatically alter community level, post-drought recovery patterns. Research was conducted during the 1993 through 1996 growing seasons at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. Study plots were twelve, 5 × 10-m non-weighing lysimeters constructed in 1992 on a gently sloping (4%) clayey range site. An automated rainout shelter was constructed to control the amount of precipitation received on 6 lysimeters during the 1992 growing season. We conclude from study results that the independent and combined effects of the imposed late spring to early fall drought and associated grazing treatments were minimal relative to soil water dynamics and aboveground net primary production although both grazing treatments reduced herbage standing crops. We attribute the absence of a strong response to the drought to its timing (i.e., late growing season) in that most herbage production in these cool-season dominated grasslands is completed by early summer. Thus, annual production processes in these grasslands avoided the major impacts of the drought. The results do not provide convincing evidence, however, that would lead us to completely reject our original hypothesis. Rather, they simply provide evidence that these grasslands are well adapted to surviving late growing season drought with or without intensive grazing by ungulates.

Key Words: Primary production, species composition, standing crop, soil water

Resumen

Esta investigación aborda la hipótesis de que la intensidad de apacentamiento durante y después de la sequía puede alterar dramáticamente, a nivel de comunidad, los patrones de recuperación post-sequía. La investigación se condujo durante las estaciones de crecimiento de 1993 a 1996 en el laboratorio de investigación sobre pastizales y ganado de Fort Keogh cerca de Miles, Montana. Las parcelas experimentales fueron 12 lisímetros livianos de 5 × 10 m construidos en 1992 en un sitio de pastizal arcilloso con pendiente suave (4%). Se construyó un abrigo automático protector de lluvia para controlar la cantidad de lluvia recibida en 6 lisímetros durante la estación de crecimiento de 1992. De acuerdo a los resultados del estudio, concluimos que los efectos combinados e independientes de la sequía impuesta a finales de primavera e inicio de otoño y asociada con los tratamientos de apacentamiento fueron mínimos relativo a la dinámica del agua del suelo y la producción primaria neta de la biomasa aérea, aunque ambos tratamientos de apacentamiento redujeron el forraje en pie. Atribuimos que la ausencia de una fuerte respuesta a la sequía se puede deber al tiempo en que esta ocurrió (por ejemplo, finales de la estación de crecimiento) en el que muchos de los pastos de estación fría, que son los que dominan estos pastizales, finalizan su producción de forraje a inicios del verano. En estos pastizales, los procesos de producción anual evitaron los principales impactos de la sequía. Los resultados no proveen una evidencia convincente, sin embargo, eso podría conducirnos a rechazar totalmente nuestra hipótesis original. Aun más, los resultados simplemente suministran evidencias de que estos pastizales están bien adaptados para sobrevivir a sequías que ocurren a fines de la estación de crecimiento con o sin apacentamiento intensivo de ungulados.

Drought is a common event in rangelands. Historically, the effects of drought on rangeland ecosystem processes have been examined by contrasting pre- and post-drought conditions in a field setting (e.g., see Albertson and Weaver 1944, 1946). Classic experimental designs that include appropriate non-drought control plots are uncommon. Notable exceptions are whole-plant honey mesquite *(Prosopis glandulosa*) studies by Ansley, et al. (1992) and a wide array of germplasm response studies (e.g., see Frank and Bauer 1991). The broad objective of this study was to examine the interactive effects of drought and livestock grazing on important rangeland variables in a "controlled" near natural rangeland setting.

This research was conducted under a cooperative agreement between USDA-ARS and the Montana Agric. Exp. Sta. and is published as contribution no. J-5176 from the Montana Agr. Exp. Sta.

Manuscript accepted 28 Sep 1998.

Our fundamental hypothesis was that grazing intensities during and following drought can dramatically alter community-level, post-drought recovery patterns and that current drought and/or post-drought livestock grazing intensities tend to suppress recovery rates (Pieper and Heitschmidt 1988, Burkhardt 1996). This hypothesis stems from an underlying assumption that drought and post-drought grazing patterns of indigenous herbivores (e.g., bison) were much different than current drought and post-drought livestock grazing patterns. It seems reasonable to assume that during periods of severe drought, large herbivores: 1) suffered severely; 2) died; and/or 3) migrated out of the affected area. But assuming death or migration were dominant responses, then it can be reasoned that animal densities following drought were well below "normal" for some period of time. Although the length of this natural, post-drought "rest" period is unknown, it would have been equal to that required for the herds to either immigrate back into the affected area or repopulate the area via natality. The specific objective of this study was to examine the interaction effects of drought and varying drought and post-drought grazing regimens on herbage growth dynamics and aboveground net primary production in a northern mixed grass rangeland.

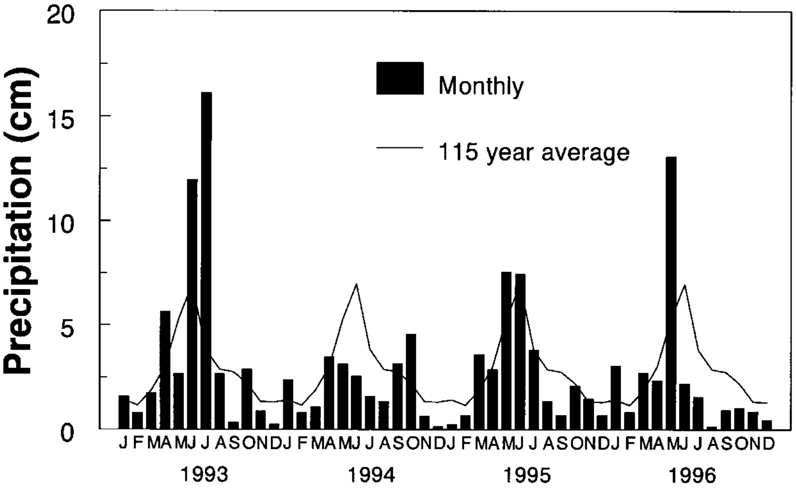

Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. (NOAA 1996).

Materials and Methods

Study Area

Research was conducted during the 1993-through 1996 growing seasons at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. (46° 22'N 105° 5'W). Regional topography ranges from rolling hills to broken badlands with small intersecting streams that flow into large permanent rivers meandering through broad nearly level valleys. The potential natural vegetation on the 22,500-ha station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mixed grass dominant (Kuchler 1964). Long-term annual precipitation averages 34 cm with about 60% received during the 150-day, mid-April to mid-September growing season (Fig. 1). Average daily temperatures range from –10° C in January to 24° C in July with daily maximum temperatures occasionally exceeding 37° C during summer and daily minimum occasionally dipping below –40° C during winter.

Study Plots and Treatments

Study plots were twelve, 5 × 10-m non-weighing lysimeters constructed in 1992 on a gently sloping (4%) clayey range site. Lysimeters were arranged perpendicularly along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups. They were constructed by filling 12 cm wide by 2 m deep perimeter trenches, and juxtaposition aboveground 12 cm wide by 15 cm tall wooden foundations, with urethane foam insulation. Each lysimeter was equipped with 2 soil water monitoring access tubes, 1 each center upslope and down-slope. In addition, each lysimeter was equipped with a surface water runoff collection system consisting of a small (about 0.2 m^2) concrete collection apron with underground plumbing for transporting water and sediment to individual fiberglass collection tanks. Lysimeter soils were Kobase silty clay loam, fine, montmorillonitic, frigid, Aridic Ustochrepts. The study area had not been grazed by livestock since 1988.

An automated rainout shelter was constructed to control amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12 × 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5 cm wide rails extending about 75 cm above the soil surface. Rails extended from top edge (i.e., upslope) to about 15 m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associated drive system, which moved the shelter across the plots.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) graze both the year of and the year after simulated drought, hereafter referred to as the 94–95 grazed treatment; 2) graze during the year of drought and rest the year after, hereafter referred to as the 94 grazed treatment; and 3) rest both the year of and the year after drought, hereafter referred to as the ungrazed treatment. These same 3 treatments were repeated in the non-drought set of lysimeters. Plots were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995. The simulated drought was imposed from late May to mid-October 1994.

Sampling Procedures

Precipitation was monitored on site using standard rain gauges. Soil water was estimated a minimum of once a month from April through October at depths of 15, 30, 60, 90, and 120 cm using a dielectric soil water probe.

Herbage standing crop was estimated monthly by clipping ten, 250 cm^2 circular quadrats per lysimeter. Five quadrats each were located randomly along 2 randomly located transects, 1 in the upslope half of the lysimeter (i.e., upslope) and the other in the down-slope half. Relative values of abundance were assigned to all species in each quadrat; however, only the most abundant species were clipped individually with most species combined into functionally similar groups. Species/species groups were: western wheatgrass (*Pascopyrum smithii* Rydb. (Love)), needle-and-thread grass (*Stipa comata* Trin. & Rupr.), warm-season perennial shortgrasses, most of which was blue grama (*Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths), with a sprinkling of buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.); other warm-season perennial grasses of which sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) was the dominant species; *Bromus* sp. which was principally Japanese brome (*Bromus japonicus* Thunb. ex Murr.) with a small amount of downy brome (*Bromus tectorum* L.); other cool-season perennial grasses of which Sandberg's bluegrass (*Poa sandbergii* Vasey) was dominant; other cool-season annual grasses of which sixweeks fescue (*Festuca octoflora* Walt.) and little barley (*Hordeum pusillum* Nutt.) were dominant; forbs; plains pricklypear cactus (*Opuntia polyacantha* Haw.); and shrubs. Herbage was dried at 60° C for a minimum of 48 hours before weighing. Amounts of live (i.e., green) and dead (i.e., brown) tissue were then estimated by hand separation.

Data Summarization and Analyses

Herbaceous aboveground net primary production was estimated by functional group (i.e., cool-season perennial grasses, cool-season annual grasses, warm-season perennial grasses, and forbs) by summing increases in live biomass. Total herbage production was estimated by summing functional group estimates.

Data were statistically analyzed using repeated measures analysis of variance procedures. Between plot (i.e., lysimeter) effects were drought and grazing treatment. The error term for testing for these effects and their associated interactions was plot within drought and grazing treatment. Years and/or dates and all associated 2 and 3-way interactions were analyzed as within plot repeated measures and were tested using full model residuals. Mean separation procedures were least significant difference contrasts. All statistically significant differences are at $P<0.05$.

The aboveground net primary production data were subjected to 3 different, yet closely related analyses so as to insure proper data interpretation. First, we analyzed all 4 years of the study as a single data set using the repeated measures analyses outlined above. Second, we analyzed the 1993 data separately from the 1994–1996 data using a 2-way (drought and grazing treatment) analysis of variance model for the 1993 data and the full repeated measures model described above for the 1995–1996 data set. Then to examine the potential impact of pre-treatment differences (i.e., 1993), we subtracted the 1993 production estimates from the 1994–1996 estimates and then subjected these adjusted means to the repeated measures analyses outlined above. This was determined to be the most appropriate way to identify statistically any pre-treatment differences.

Results

Precipitation and Soil Water

Amounts and patterns of annual precipitation varied widely among years (Fig. 1). During the pre-treatment year of 1993, an abundance of late spring and early summer precipitation resulted in total annual precipitation being 38% above the long-term norm of 34.1 cm. In contrast to 1993, annual precipitation during 1994 was 24.7 cm, 24% below normal, with precipitation from 1 May to 31 October, being only 16.3 cm as compared to the long-term average for this period of 27.1 cm. Total precipitation received on the drought plots during 1994 was 10.7 cm with 2.3 cm received during the months of June through October. Total annual precipitation during both the post-drought year of 1995 and the post-treatment year of 1996 was near the long-term average of 34 cm. However, patterns of distribution were quite different as the

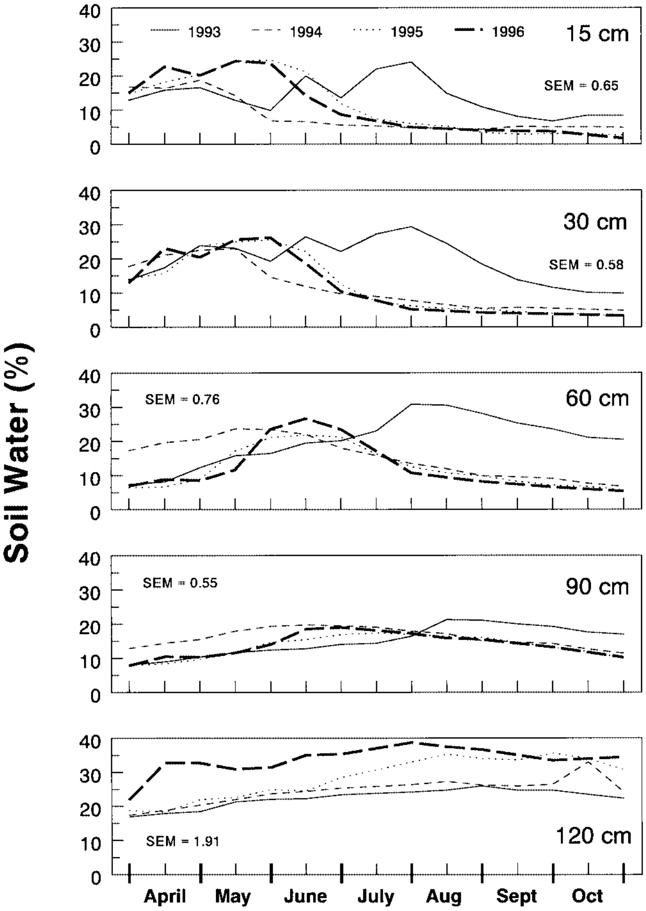

Fig. 2. Percentage soil water during the 1993 through 1996 growing seasons at 5 depths. Traces are average of the 3 grazing and 2 drought treatments as neither the main effect of grazing nor drought treatment was statistically significant.

1995 monthly pattern was similar to the long-term norm whereas the 1996 pattern was dominated by a near 200% above normal rainfall in May.

Analyses of the soil water data by depth showed impacts of the imposed 1994 drought and grazing treatments were minimal with the only statistically significant main effects being year and date. Although 32 of the 50 interaction effects included in the 5 analyses were significant, only 12 explained >2% of the variability. No definitive patterns emerged from an examination of these interactions other than the date by year interaction which was significant in all 5 depth analyses. Thus, data were combined across drought and grazing treatments for presentation (Fig. 2).

The year effect was caused by greater amounts of soil water at the 15 through 60 cm depths throughout the summer and fall of 1993 than any other year. This was largely because of the greater amount of precipitation received during June and July 1993 than other years (Fig. 1). Also, as expected, there were generally greater amounts of soil water at the 120-cm depth than the shallower depths, and magnitude of seasonal fluctuations decreased as depth of soil water increased. It is also interesting to note that soil water content at 120 cm tended to increase over the 4-year study period. We suspect this was the result of downward leakage of water around the soil water monitoring access tubes as they passed through the Kobase soil's highly impermeable clay pan located at a depth of about 1 m.

Aboveground Biomass Dynamics

Analyses of live, dead, and live + dead (i.e., total) biomass by functional group (i.e., cool-season perennial grasses, cool-season annual grasses, warm-season perennial grasses, and forbs) resulted in few significant main effects and many significant interactions. Still, interpretable, biologically meaningful patterns did emerge when standing crop data were examined within years rather than across years (Fig. 3).

In 1993, the pre-treatment year, the main effects of date and drought treatment were significant relative to total standing crop. Averaged across dates, standing crop in the grazing treatment plots allocated to the scheduled 1994 drought treatment was 2,018 kg ha^{-1} as compared to a 2,331 kg ha^{-1} average for the non-drought allocated plots. This difference was largely the result of lesser amounts of cool-season perennial grasses in the drought than non-drought plots (572 vs. 1,237 kg ha^{-1}). The date effect reflected normal seasonal growth patterns (Fig. 3). The larger than normal standing crops were the result of exceptionally high rainfall (Fig. 1).

In 1994, the year the drought was imposed and the grazing treatments initiated, total standing crop was significantly altered by drought, grazing treatment, and date, and by the interaction of grazing treatment by date. The significant grazing treatment by date interaction resulted from the effects the early June and July grazing events had on standing crops during the remainder of the year (Fig. 3). For example, averaged across the 2 drought treatments, total standing crop from July through October was about 2,000 kg ha^{-1} less in the 8 grazed than 4 ungrazed treatment plots following average declines of 1,387 and 778 kg ha^{-1} during the June and July grazing events, respectively. The significant drought effect arose because average standing crop in the drought treatments was 1,735 kg ha^{-1} as compared to 2,084 kg ha^{-1} in non-drought treatments. Averaged across dates, standing crop in the 2 grazed treatments averaged 1,580 kg ha^{-1} as compared to 2,567 kg ha^{-1} in the ungrazed treatment. The date effect was again the result of normal seasonal growth dynamics.

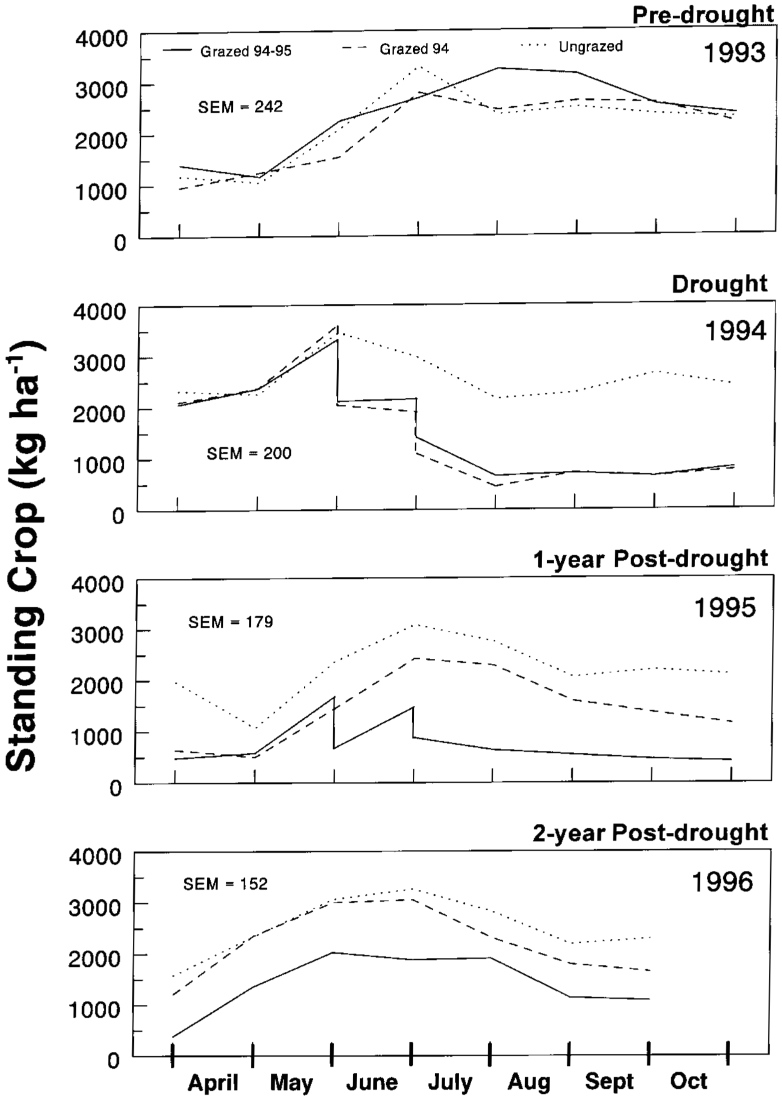

Fig. 3. Herbage standing crops (kg ha^{-1}) for the 3 grazing treatments during the 1993 through 1996 growing seasons. Traces are average of 2 drought treatments.

In 1995, the first post-drought recovery year, total standing crop was again significantly altered by the main effects of the 1994 drought, grazing treatment, and date, and by the interaction of grazing treatment and date. However, the grazing treatment by date interaction was more complex than in 1994 in that in the early portion of the growing season it was the result of both 1994 grazing treatments whereas in the latter part of the season it was largely the result of just the 94-95 grazing treatment (Fig. 3). Again, average standing crop in the 1994 drought plots was less than in non-drought plots (1,259 vs. 1,673 kg ha^{-1}) and, as expected, varied significantly among grazing treatments being least in 94-95 grazed (782 kg ha^{-1}) and greatest in the ungrazed (2,196 kg ha^{-1}) with 94 grazed intermediate (1,422 kg ha^{-1}). The date effect was, as in previous years, the result of normal seasonal growth dynamics.

In 1996, the second post-drought recovery year and the first wherein no plots were grazed regardless of previous treatment, only the main effects of grazing treatments and date were significant. The grazing treatment effect arose because average standing crop of 1,398 kg ha^{-1} in the 94-95 treatment was significantly less than the 2,353 kg ha^{-1} average for the 94 grazed and the ungrazed treatment. There was no difference between the 94 grazed and the ungrazed treatments. Date effects were, as in previous years, a reflection of normal seasonal growth dynamics (Fig. 3).

Aboveground Net Primary Production

Results from the analyses of the adjusted production data (i.e., 1993 means subtracted from 1994–1996 means) supported the data interpretation arising from the analyses of the unadjusted means. The only difference between the 2 analyses was that the main effects of drought treatment on total, cool-season perennial grass, and annual grass production was significant (P<0.05) in the analyses of the unadjusted means but not the adjusted means (P>0.18). The main effects of year and all interaction effects were identical. Insights arising from these differences are duly noted in the presentation of results below.

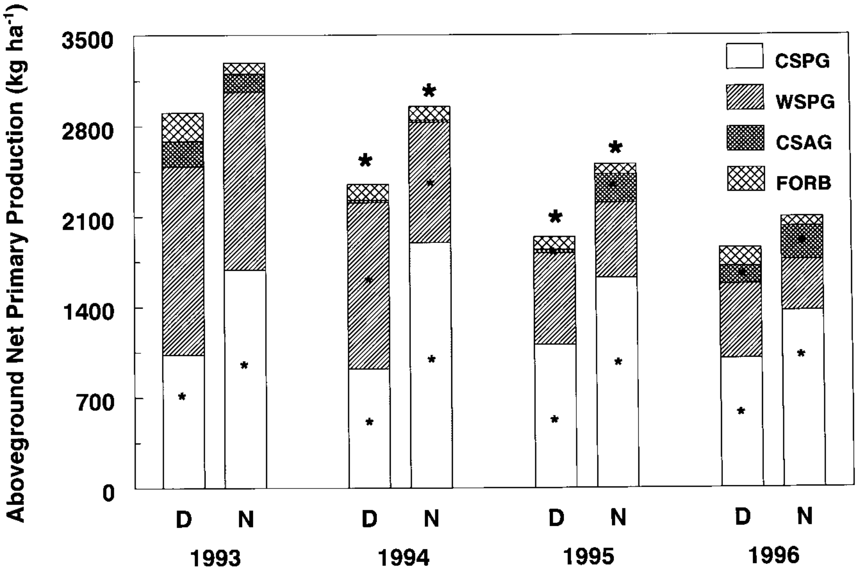

Fig. 4. Aboveground net primary production estimates (kg ha-1) for drought (D) and non-drought (N) treatments for 1993 through 1996. Species groups within a year with asterisks are significantly different @ P < 0.05. Totals within a year with asterisk above column at significantly different @ P < 0.05.

Analyses of the 1993 production data showed there were no differences among plots in total production averaging 3,097 kg ha^{-1}. However, some differences among plots were found in cool-season perennial grass and forb production (Fig. 4). Cool-season grass production was less in plots allocated for the 1994 drought treatment than non-drought plots (1,030 vs. 1,687 kg ha^{-1}) largely because of less western wheatgrass in drought than non-drought plots. Forb production in the drought 94–95 grazing treatment was several fold greater than all other grazing treatment plots (580 vs. 66 kg ha^{-1}). This was largely because we harvested 18 g of forbs from 1 of the 10 randomly located 250 cm^{2} sample quadrat (i.e., 1,434 kg ha^{-1}) on 1 date in 1 of the two, 94–95 grazed treatment plots. As a result, forb production averaged 580 kg ha^{-2} in the drought 94–95 grazed treatment as compared to only 66 kg ha^{-2} in the 5 other treatments.

Analyses of total production (i.e., sum of functional groups) from 1994 through 1996, showed significant drought and year effects with no interactions. Averaged across years and grazing treatments, total production in drought plots was 2,049 kg ha^{-1} as compared to 2,518 kg ha^{-1} in non-drought plots. The primary difference between the drought and non-drought plots was in amounts of cool-season perennial grasses (1,009 vs. 1,629 kg ha^{-1}) (Fig. 4). However, this difference was a carryover of pretreatment differences in production rather than the imposed 1994 drought. This was confirmed by the loss of significant drought treatment effects on total and cool-season perennial grass production when 1994–1996 means were adjusted by subtracting 1993 means. There was also less annual grass production in drought (61 kg ha^{-1}) than non-drought plots (164 kg ha^{-1}) depending upon year. But again, this was largely because of pre-treatment differences in annual grass production.

Surprisingly, total production was greater during the drought year of 1994 than the 2 post-drought years of 1995 and 1996. Averaged across drought and grazing treatments, production averaged 2,651 kg ha^{-1} in 1994 as compared to an average of 2,100 kg ha^{-1} in 1995 and 1996 (Fig. 4). These differences were largely the result of a significant decline in warm-season perennial grass production from 1994 through 1996 which averaged 1,110, 645, and 486 kg ha^{-1}, respectively. On the other hand, there was a significant increase in cool-season annual grass production from 17 kg ha^{-1} in 1994 to 197 kg ha^{-1} in 1996. Annual grass production in 1995 was intermediate to 1994 and 1996 averaging 123 kg ha^{-1}.

Although grazing treatment was not significant in any of the herbage production analyses, there were 2 significant year by grazing treatment effects. The first was warm-season grass production

Table 1. Two-way interaction effects of year and grazing treatment on aboveground net primary production (kg ha^{-1}) of warm-season perennial grasses. Means are averaged across drought treatments.

Year	Grazing Treatments 94–95	94	ungrazed
	- - - - - - - - - (kg ha^{-1}) - - - - - - - - -		
1994	1,220$^{1}_{a}$	1,329$_{a}$	781$_{b}$
1995	675$_{b}$	559$_{b}$	701$_{b}$
1996	384$_{c}$	455$_{bc}$	619$_{bc}$

[1] Means in a row or column followed by same letter are not significantly different at P=0.05.

(Table 1) in which the annual production pattern indicated grazing reduced warm season grass production regardless of drought treatment. The second year by grazing treatment interaction effect was cool-season annual grass production (Table 2). In this instance, it appeared that grazing during drought had no effect on production whereas grazing the year after drought tended to decrease annual grass production.

Discussion and Conclusions

Previous research on Northern Great Plains rangelands has shown generally that grazing is a secondary factor affecting ecosystem processes whereas drought is a primary factor (Whitman et al. 1943, Hurt 1951, Reed and Peterson 1961, Olson et al. 1985, Biondini and Manske 1996, Biondinin et al. 1998). Our results support this conclusion well with regards to grazing impacts but not as it relates to drought. Quite honestly, the imposed drought did not impact the variables we examined to the extent hypothesized. Evidence supporting this conclusion are that the independent and combined effects of the imposed drought and grazing treatments were minimal relative to soil water dynamics (Fig. 2) and aboveground net primary production (Fig. 4). Granted, grazing treatments did reduce herbage standing crops (Fig. 3), but that was as expected.

We believe the primary reason the drought in this study had minimal impact on post-drought recovery patterns is most likely related to timing of the drought (i.e., late growing season). These grasslands are dominated by cool-season plant species that complete most of their growth by late spring and early summer (Heitschmidt et al. 1995, Dodd et al. 1982); thus, plants only need sufficient amounts of soil water until late spring to complete their "normal" production cycle. In this study, there was apparently a sufficient soil water reserve when the drought was initiated (i.e., late May, see Fig. 2) for the annual production cycle to be completed. A compounding factor that may have dampened our ability to detect drought effects, was that the amount of ambient precipitation falling on non-drought plots during the imposed drought was well below normal (Fig. 1). Thus, late season production on non-drought plots may have been curtailed by natural drought although magnitude of curtailment did not appear to be great since annual production in 1994 was similar to 1995 and 1996 (Fig. 4).

The positive effect that the 1994 drought had on warm-season grass production (Fig. 4) was unexpected. Logically, one would assume that a late spring drought would depress production of warm-season species more than cool-season species. We offer no explanation for these results.

The general absence of grazing treatment effects on primary production was also unexpected although in retrospect we believe timing of drought greatly dampened the interaction of drought and grazing treatment. An exception was warm-season perennial grass production wherein grazing during the 1994 drought appeared to initiate a declining post-drought production trend regardless of post-drought grazing treatment (Table 1). We hypothesize this was because our June and July flash grazing tactics somehow enhanced warm-season grass growth. But since this was not manifested in 1995 in the 94–95 grazed treatment, definitive conclusions as to causal factors for the 1994 results are difficult.

We hypothesize that the causal factors associated with the interaction of year and grazing treatment on annual grass production (Table 2) were most likely related to both climatic growing conditions and the impacts that level of ground cover has been shown to have on Japanese brome production in other regions (Whisenant 1990, Heitschmidt et al. 1982). However, there was no clear evidence supporting any single explanation; thus, we choose to limit our speculation.

The results of this study also provide strong support for the need for pre-treatment baseline data in field studies. For example, consider what conclusions might have been drawn from the results without pre-treatment data. The most obvious conclusions would have been that the drought depressed total herbage production substantially, even up to 2 years after the drought and that the major contributing factor was a substantial reduction in cool-season perennial grass production. However, inclusion of the 1993 data in our interpretation dampens greatly the magnitude of the effect of the drought on both total production and functional group's contributions to the total.

Table 2. Two-way interaction effects of year and drought treatment on aboveground net primary production (kg ha^{-1}) of annual grasses. Means are averaged across drought treatments.

Year	Grazing Treatments 94–95	94	ungrazed
	- - - - - - - - - (kg ha^{-1}) - - - - - - - - -		
1994	23$^{1}_{a}$	10$_{a}$	18$_{a}$
1995	150$_{b}$	123$_{b}$	98$_{ab}$
1996	110$_{ab}$	239$_{c}$	244$_{c}$

[1] Means in a row or column followed by same letter are not significantly different at P=0.05.

And lastly, the results from this study's non-drought, ungrazed plots are very similar to findings from similar studies conducted on indigenous Northern Great Plains rangelands in terms of seasonal growth dynamics and productivity capacity (Lewis et al. 1971, Coupland 1974, Laurenroth et al. 1975, Lauenroth and Whitman 1977, Sims and Singh 1978a, 1978b, Dodd et al. 1982, Singh et al. 1983, Heitschmidt et al. 1995). Normally, peak standing crop in the Northern Great Plains occurs between early June and mid-July depending upon plant species composition and pattern and amount of precipitation. Our data fit this pattern well (Fig. 3). Similarly, estimated aboveground herbage production for this region ranges between 1,600 and 4,000 kg ha^{-1} depending upon site, year, and methodology (Singh et al. 1983, Heitschmidt et al. 1995, Biondini and Manske 1996, Biondini et al. 1998). The results of this study support these generalizations well (Fig. 4).

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52:447–453 September 1999

Early summer grazing effects on defoliation and tiller demography of prairie sandreed

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Abstract

Grazing strategies should be designed to maintain vigorous populations of plant species critical for livestock production, wildlife habitat, and/or ecosystem functions. Treatments consisting of 5- to 7-day, mid-month grazing periods in June or July at 16, 32, or 48 animal unit days (AUD) per ha, were replicated 3 times and applied to the same pastures in 1995 and 1996 to quantify cattle use and tiller recruitment and mortality of prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.], a rhizomatous species characterized by dispersed populations of tillers. Cumulative grazing pressure (AUD Mg^{-1}) was used to quantify treatments because of differences in phytomass among pastures and dates. Grazing pressure ranged from 10 to 90 AUD Mg^{-1} and accounted for 69, 61, and 77% of the variation in percentage of tillers grazed, mean defoliation of grazed tillers, and use of prairie sandreed, respectively. As grazing pressure increased from 10 AUD Mg^{-1}, percentage of tillers grazed increased from 48 to 90%; defoliation of grazed tillers increased from 54 to 74%; and utilization of prairie sandreed increased from 27 to 67% at plateaus beginning at 50 to 60 AUD Mg^{-1}. When spring precipitation was above average, 45 to 55% use in June or July increased tiller densities, however, these increases were not sustained or repeated in the following year with average precipitation. Utilization was 50% at 28 AUD Mg^{-1} and 60% at 40 AUD Mg^{-1}. Relatively large increases in utilization per-unit-change of grazing pressure below 20 AUD Mg^{-1} indicated that yearling cattle selectively grazed prairie sandreed. The high degree of correlation between percentage of prairie sandreed tillers grazed and use of prairie sandreed (R^2 = 0.91 in June and 0.90 in July) suggests that percentage of grazed tillers can be used to monitor early-summer use of this species in the Nebraska Sandhills.

Key Words: stocking rate, grazing pressure, tiller recruitment and mortality, *Calamovilfa longifolia*

Resumen

Las estrategias de apacentamiento deben diseñarse para mantener poblaciones vigorosas de las especies de plantas que son críticas para el ganado, hábitat de la fauna silvestre y/o funciones del ecosistema. Los tratamientos consistieron en períodos de apacentamiento de 5 a 7 días a mediados de mes durante Junio y Julio, con cargas animal de 16, 32 o 48 unidades animal día (UAD) por hectárea. Los tratamientos se repitieron 3 veces y se aplicaron en los mismos potreros durante 1995 y 1996 para cuantificar el uso del ganado y el restablecimiento y mortalidad de hijuelos del zacate "Prairie sandreed" [Calamovilfa longifolia (Hook) Scribn], una especie rizomatosa caracterizada por poblaciones dispersas de hijuelos. Debido a las diferencias de fitomasa entre potreros y fechas, la presión de apacentamiento acumulativa (UAD Mg^{-1}) se utilizó para cuantificar los tratamientos. La presión de apacentamiento vario de 10 a 90 UAD Mg^{-1} y contribuyo con el 69, 61 y 77% de la variación de las variables: porcentaje de hijuelos apacentados, promedio de defoliación de los hijuelos apacentados y uso del "Prairie sandreed" respectivamente. Conforme la presión de apacentamiento se incremento de 10 UAD Mg^{-1}, el porcentaje de hijuelos apacentados se incremento de 48 a 90%; la defoliación de hijuelos apacentados incremento de 54 a 74% y la utilización del "Prairie sandreed" se aumento de 27 a 67% iniciando la estabilización de la curva entre 50 a 60 UAD Mg-1. Cuando la precipitación de primavera fue mayor que el promedio, el uso entre el 45 a 55% en Junio o Julio incremento las densidades de hijuelos, sin embargo, estos incrementos no se sostuvieron o repitieron en el siguiente año con la precipitación promedio. Con 28 UAD Mg^{-1} la utilización fue del 50% y del 60% con 40 UAD Mg^{-1}. El incremento relativamente grande en la utilización por unidad de cambio de la presión de apacentamiento abajo de 20 UAD Mg^{-1} indico que el ganado de año apacentó selectivamente el "Prairie sandreed". El alto grado de correlación entre el porcentaje de hijuelos del "Prairie sandreed" apacentados y el uso del "Prairie sandreed" (R^2 = 0.91 en Junio y 0.90 en Julio) sugiere que el porcentaje de hijuelos apacentados puede ser utilizado para monitorear el uso de esta especie a inicios del verano en el Nebraska Sandhills.

Effects of stocking rate, grazing pressure, and/or date of grazing on defoliation of individual species in native plant communities have been investigated extensively (Butler and

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Research was partially supported by the Anna H. Elliott Fund, University of Nebraska Foundation. Published as Paper 12225 , Journal Series, Nebraska Agricultural Research Division.

Manuscript accepted 6 Dec. 1998.

Briske 1988, Gillen et al. 1990, Jensen et al. 1990, Hart et al. 1993, Allen and Marlow 1994, Derner et al. 1994). However, most grazing systems used on semi-arid rangelands are not designed for specific plant species. Successful systems use moderate stocking rates and/or growing-season deferment of adequate length and frequency to minimize and compensate for grazing damage to vegetation (Heady 1984, Ralphs et al. 1990). Knowledge of critical grazing pressure and critical grazing dates for key plant species should be incorporated into grazing systems (Zhang and Romo 1995, Reece et al. 1996). Additionally, efficient methods are needed for monitoring livestock use of key forage species to optimize grazing strategies (Manley et al. 1997, Ortega et al. 1997, Taylor et al. 1997).

Effects of early-summer stocking rates on livestock use and tiller dynamics have not been reported for prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.], a key forage species throughout the 4.9 million ha of Nebraska Sandhills and the sandy prairie soils of the northern and central Great Plains (Lodge 1963, Welch 1968, Aase and Wight 1973, GPFA 1986). In the Nebraska Sandhills, prairie sandreed can provide 25 to 40% of the herbage produced on upland range sites in good to excellent condition (Nichols et al. 1984). Tillering response of grasses to defoliation is affected by selective herbivory, environment, phenological stage, and severity and frequency of defoliation (Briske and Richards 1995); therefore, it is often necessary to evaluate species responses to grazing within given ecosystems.

In Nebraska, length of time that cattle are on rangeland during the summer grazing season has declined to avoid reduced gains and/or reduced cow condition when forage quality declines with advanced plant maturity. Additionally, interest in placing relatively heavy yearlings on high-quality, early-summer forage for 1 to 3 months before they enter feedlots has increased. In contrast to the ability of tallgrasses in humid environments to tolerate intensive early-season stocking (Smith and Owensby 1978, McCollum et al. 1990), heavy grazing (1.5X) in June or July causes measurable reductions in total organic reserves in prairie sandreed (Reece et al. 1996). Our objective was to quantify defoliation processes and effects on tiller demography of prairie sandreed over a wide range of grazing pressure to supplement an ecological data base for the development of grazing strategies in the Nebraska Sandhills. Three stocking rates and 2 grazing dates were used to produce an array of grazing pressures. We hypothesized that (1) use of prairie sandreed would increase at a constant rate as grazing pressure increased, and (2) tiller recruitment and mortality would increase as defoliation increased.

Materials and Methods

The study was conducted on sands range sites in good to excellent condition at the University of Nebraska, Gudmundsen Sandhills Laboratory (GSL) located near Whitman, Nebr. Prairie sandreed, sand bluestem (*Andropogon hallii* Hack), and little bluestem (*Andropogon scoparius* Michx.) were co-dominant species on these sites (Great Plains Flora Association 1986). Long-term average annual precipitation is 560 mm (National Oceanic and Atmospheric Administration 1996). Soils are Valentine fine sands (mixed, mesic Typic Ustipsamments).

Experimental units were individual 1.0-ha pastures. Twenty-one pastures were separated into 3 blocks based on frequency of occurrence of species in fifty, 50 × 50-cm quadrats randomly located on stratified transects in each pasture in May 1995. Six stocking rate by grazing date treatments and an ungrazed control were randomly allotted to pastures within each block. Grazing treatments consisted of 1, 5- to 7-day, mid-month grazing period in June or July at 16, 32, or 48 AUD ha^{-1}, representing light (0.5X), moderate (1.0X), and heavy (1.5X) seasonal stocking rates. Yearling cattle were weighed after an overnight stand without food and water and allocated to treatments by weight to provide equal total weights of cattle for replications within stocking rate treatments. Animal weights were divided by 454 kg to estimate animal unit (AU) equivalents. The number of yearlings per pasture ranged from 4 to 12. Grazing treatments were applied to the same pastures during 1995 and 1996. Pastures in this study were used for grazing research from 1988 to 1991 (Reece et al. 1996). All pastures were rested in 1992 and 1994. Pastures were stocked at 49 AUD ha^{-1} from June to October 1993.

Twenty, 20 × 50-cm quadrats were located systematically in each pasture over a 20 × 20-m grid in late-May 1995. A quadrat was placed near each grid point where a minimum of 7 current-year prairie sandreed tillers occurred. Quadrats were marked permanently with landscaping staples and numbered aluminum tags. Survival of current-year tillers with 1 or more fully expanded leaf blades was censused in early June, early July, early August, late August, and early October. The base of new tillers was loosely wrapped with a different color-coded telephone wire for each sampling date. Dead tillers were marked with latex paint and the wire was removed after initial census date was recorded. All wires were removed from 1995 tillers in late May 1996, and biennial tillers were counted. The census procedure was repeated in 1996. A data set of demographic differences was generated by subtracting mean responses for ungrazed control pastures from mean responses for grazed treatments within each block.

Before grazing treatments were applied, current-year standing herbage was estimated by clipping all vegetation at ground level in ten, 25 × 100-cm randomly located quadrats per pasture. Previous years growth and plant species not grazed by cattle were discarded. Species not grazed by cattle in June or July included six weeks fescue, (*Festuca octoflora* Walt.), green sagewort (*Artemisia dracunculus* L.), western ragweed (*Ambrosia psilostachya* DC.), prickly pears (*Opuntia* spp. P. Mill.), pincushion cactus [(*Corypanthia vivipara* (Nutt.) Britt. & Rose], and prairie wild rose (*Rosa arkansana* Porter) (Northup 1993). Palatable herbage was oven dried at 60°C for 48 hours and weighed to the nearest 0.1 g to determine dry matter yield. Grazing pressure was expressed as animal unit days per metric ton of current-year palatable herbage measured at the beginning of grazing periods (AUD Mg^{-1}).

Defoliation was estimated from marked tillers in 10 quadrats randomly selected from the 20 permanently marked 20 × 50-cm quadrats in each pasture used to monitor tiller demography. Distribution of tiller biomass over tiller height was measured in June and July to estimate percentage defoliation based on stem-diameter class and remaining stem height. About 100 ungrazed tillers were randomly selected and clipped at ground level at each of 20 sample areas outside the pastures during each grazing period and sorted into 5 stem-diameter classes: <1 mm, 1–2 mm, 2–3 mm, 3–4 mm, and >4 mm. For each sample area, tillers within stem-diameter classes were tied into bundles, with stem bases flush at one end. Bundles were balanced on a narrow edge to determine average remaining height at which 50% of the herbage would be removed. The bundle was cut in half at the balance point. Top and bottom half bundles were balanced and measured to determine average remaining stem heights for 25 and 75% defoliation. Equations fit to these data with regression analysis ($R^2 \geq 0.90$) were used to estimate defoliation of each grazed prairie sandreed tiller in each quadrat when yearlings were removed from pastures. Height-weight relations were similar for defoliated and nondefoliated prairie sandreed tillers because the upright growth habit and distance among the dispersed tillers of this species resulted in top-down defoliation when cattle grazed prairie sandreed. The summation of tiller numbers in each stem-diameter class multiplied by mean tiller weight for respective stem-diameter classes was used to estimate current-year prairie sandreed herbage in each quadrat. Percentage defoliation of each grazed tiller multiplied by mean tiller weight for the respective stem-diameter class was summed and divided by current-year prairie sandreed herbage to estimate utilization of prairie sandreed populations in each quadrat.

Data were analyzed as a split-plot in time with the General Linear Models Procedure (SAS 1985). Pre-planned contrasts were used to test for differences between control and grazed treatments, for differences between grazing dates, and to test for linear and quadratic effects of grazing pressure (Cullan 1998). Treatment effects were considered significant at $P \leq 0.05$. When significant grazing pressure effects occurred, regression analysis was used to fit equations to 36 grazed pasture-by-year means for percentage tillers grazed, percentage defoliation of grazed tillers, and use of prairie sandreed populations. All 3 defoliation characteristics plateaued. Data within the plateau were fit with a non-significant line estimated by the mean of values within the plateau. Regression analysis also was used to fit equations to 18 grazed pasture-by-year means for the relationship between use of prairie sandreed populations (dependent variable) and percentage of prairie sandreed tillers grazed (independent variable) in June and in July.

Results and Discussion

Available Herbage

When grazing treatments began in mid-June, yield of current-year, palatable herbage was 48% greater in 1995 than in 1996 (860 compared to 580 kg ha^{-1}), which was associated with 87% more precipitation during March to June 1995 than in 1996. Mean air temperatures during April to May 1995 were 5 to 6°C below 30-year averages while temperatures and precipitation in 1996 were similar to long-term averages. Mean current-year herbage when grazing started in July pastures was about 1,360 kg ha^{-1} in both years. Current-year herbage in pastures ranged from 360 kg ha^{-1} in mid-June to 1,630 kg ha^{-1} in mid-July. A correspondingly wide range of cumulative grazing pressure (10 to 90 AUD Mg^{-1}) resulted from the different combinations of pastures, grazing dates, and stocking rates.

Among the 3 co-dominant grass species, prairie sandreed was the most uniformly distributed within pastures with a mean frequency of occurrence ≥ 78% in all pastures and a frequency of 90 to 100% in 18 of 21 pastures (Fig. 1). Prairie sandreed produces populations of dispersed tillers in which rhizome tillers may emerge more than 30 cm from parent tillers (Maun 1985). In contrast, rhizomes of sand bluestem are intermediate in length and little bluestem is a bunchgrass (Weaver 1965). The frequency distribution of sand bluestem for pastures was intermediate between prairie sandreed and little bluestem and the distribution of both bluestems varied measurably among pastures (Fig. 1). Additionally, the presence of 20 other species of native graminoids and 45 species of native perennial forbs in these pastures (Northup 1993) provided the opportunity for a measurable diversity of species to be associated with prairie sandreed, within and among pastures. In

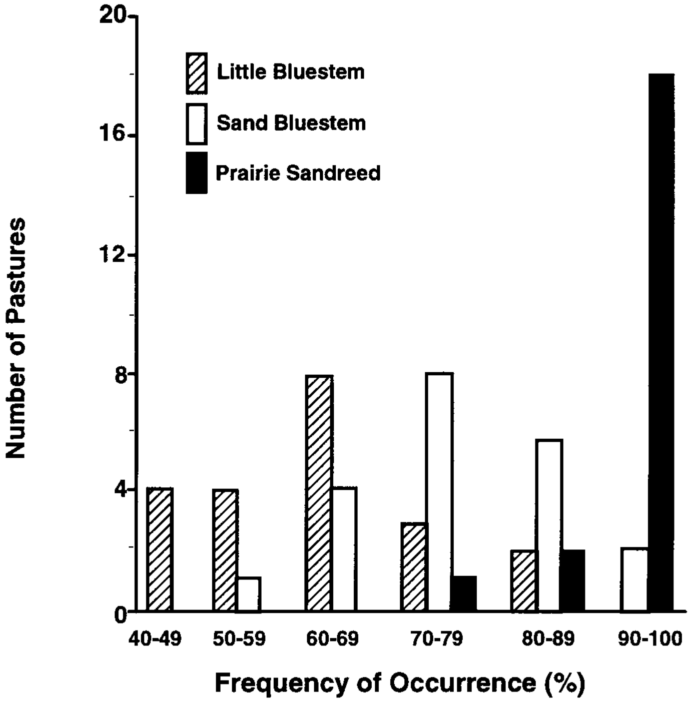

Fig. 1. Distribution of mean frequencies of occurrence for pastures for little bluestem, sandbluestem, and prairie sandreed in 50, 0.25-m^2 quadrats per pasture at the Gudmundsen Sandhills Laboratory, near Whitman, Nebr., in May 1995.

a preceding, 3-year study in these pastures, prairie sandreed produced about 20% of the current-year herbage available in June and July each year while sand bluestem and little bluestem collectively produced 23 to 50% of the herbage available in June or July (Northup 1993).

Defoliation of Prairie Sandreed

Prairie sandreed tiller populations are predominantly vegetative throughout the growing season at The Gudmundsen Laboratory (GSL) (Hendrickson et al. 1997). Percentage of tillers grazed increased rapidly from about 48% at 10 AUD Mg^{-1} to 78% at 30 AUD Mg^{-1} (Fig. 2a). Above 50 AUD Mg^{-1}, cattle consistently grazed about 90% of the prairie sandreed tillers. Grazing pressure accounted for 69% of the variation in percentage of tillers grazed in the 18 pastures during 2 years. While grazing pressure accounted for only a small amount of variation in occurrence of defoliation of key species in a tallgrass prairie in Oklahoma, Gillen et al. (1990) reported relatively wide ranges in percentage of tillers grazed over a narrow range in grazing pressure. Percentage of tillers grazed increased from 35 to 100% for big bluestem (*Andropogon gerardii* Vitman) and from 20 to 80% for little bluestem when grazing pressure increased from 7 to 33 AUD Mg^{-1}.

Mean defoliation of grazed tillers increased about 2% for each 5 AUD Mg^{-1} increase in grazing pressure, from 54% at 10 AUD Mg^{-1} to a plateau of about 74% from 58 to 90 AUD Mg^{-1} (Fig. 2b). Grazing pressure accounted for 61% of the variation in mean defoliation of grazed tillers among pastures. Part of the remaining variation may have been caused by the top-down grazing of this species that resulted in relatively small variation in grazed height within grazing treatments (Northup 1993, Cullan 1998) regardless of stem-diameter class. Tiller height was directly proportional to stem diameter (Cullan 1998). Consequently, percentage defoliation of grazed tillers with stem diameters > 4 mm was greater than defoliation of tillers with 1 to 2 mm stem diameters when plants were grazed to the same remaining height.

Grazing pressure accounted for 77% of the variation in utilization of prairie sandreed populations among pastures (Fig. 2c). The average rate at which utilization increased was about 5% per 4 AUD Mg^{-1} from 10 to 30 AUD Mg^{-1} compared to about 5% per 10 AUD Mg^{-1} from 30 to 60 AUD Mg^{-1} (Fig. 2c). Consequently, 50% use of prairie sandreed occurred relatively rapidly at 28 AUD Mg^{-1} during early-summer grazing, although 60% use required an additional 12 AUD Mg^{-1} or a 43% increase in cumulative grazing pressure. We reject our hypothesis that use of prairie sandreed increases at a constant rate as cumulative grazing pressure increases and conclude that cattle preferentially graze this species in June and July.

The potential for plant growth during grazing periods to cause errors in cumulative grazing pressure calculations was greater in June compared to July because of lower amounts of current-year herbage and relatively higher rates of plant growth. However, comparable levels of dry-matter intake by cattle at equal stocking rates would have reduced leaf area more rapidly in June than in July and may have limited the potential of plant growth in June to effect grazing pressure estimates. Average growth rates in July (Northup 1993) would cause less than 5% error in cumulative grazing pressure calculations for 5-to 7-day periods. The relatively high correlation of data from June and July during 2 years with measurable differences in precipitation suggests standing crop estimates at the beginning of short grazing periods are adequate for estimating cumulative grazing pressure in this ecosystem.

Physiologically, damage to growing grasses is generally stated to be minimal until defoliation exceeds 50 to 60% (Crider 1955, Launchbaugh 1967, Ryle and Powell 1975). Mean use of prairie sandreed plateaued at about 67% from 60 to 90 AUD Mg^{-1} which is measurably

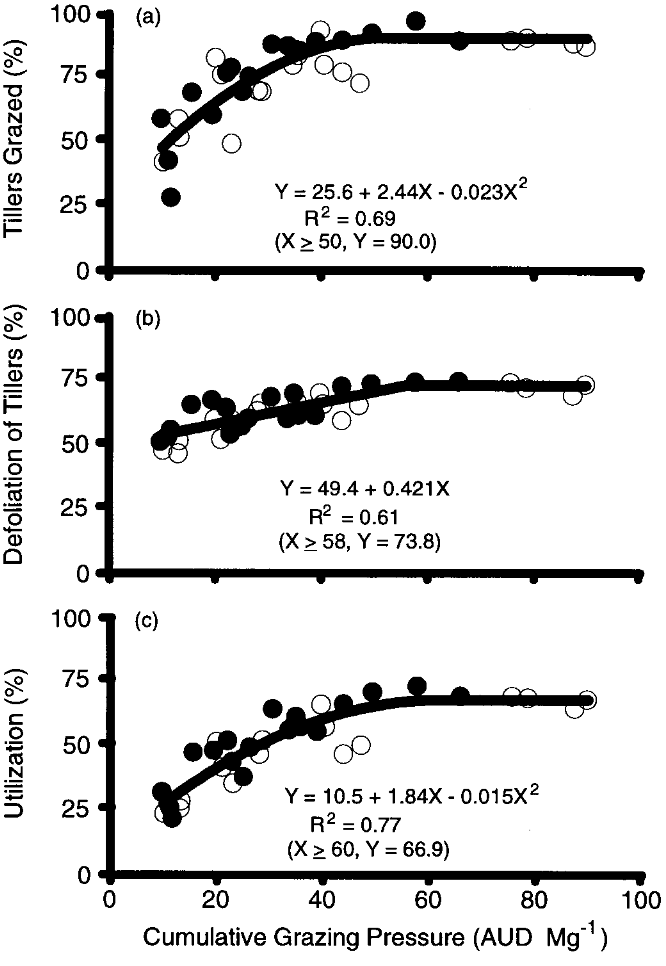

Fig. 2. Effects of cumulative grazing pressure on percentage of tillers grazed (a), percentage defoliation of grazed tillers (b), and utilization of prairie sandreed in pastures at the Gudmundsen Sandhills Laboratory, near Whitman, Nebr., after grazing in mid-June or mid-July in 1995 (°) and 1996 (•).

higher than reported for grazing use of key management species in other Great Plains range ecosystems (Hart and Balla 1982, Gillen et al. 1990). Translocation of nutrients through rhizomes from ungrazed to grazed tillers may be an important mechanism of grazing tolerance in prairie sandreed because mean defoliation of grazed tillers was greater than 50% over the entire range of grazing pressure in this study. If tolerance of prairie sandreed to grazing is primarily clonal (Stout and Brooke 1985) compared to an individual tiller response, measurable effects of grazing may occur between 50 and 60% use when the ratio of ungrazed to grazed tillers decreases from 1:4 to less than 1:7. When use of prairie sandreed plateaued at 67% the ratio of ungrazed to grazed tillers was 1:10.

Given the large differences in herbage that can occur among pastures and years, and the pronounced effect of cumulative grazing pressure on utilization, stocking rate is a poor criterion for effective early-summer grazing management decisions for prairie sandreed. It is also unlikely that animal condition could be used as an index for proper use of prairie sandreed because relatively high levels of forage quality during early summer (Hendrickson et al. 1997, Northup and Nichols 1998) could result in high levels of animal performance at relatively high grazing pressures (Hart et al. 1983).

An efficient method of monitoring utilization of prairie sandreed is needed when the potential for high grazing pressure occurs in June or July. Utilization of prairie sandreed was highly correlated (R^2 = 0.91 in June and 0.90 in July) with percentage of prairie sandreed tillers grazed over a wide range in species composition and grazing pressures (Fig. 3). Percentage defoliation of grazed tillers was greater in June compared to July (Cullan 1998) because of higher grazing pressure (Fig. 2b). Consequently, when utilization of prairie sandreed populations was below 40%, fewer tillers were grazed at comparable levels of use in June compared to July, i.e., 42% of tillers grazed at 35% use in June compared to 62% of tillers grazed at 35% use in July. However, the percentage of tillers grazed in each month converged rapidly to 72% in June and 78% in July at 50% use. It should be possible to estimate use of prairie sandreed in June or July from percentage of tillers grazed with a high degree of repeatability. Grazing pressure can be used to select dates at which monitoring should begin.

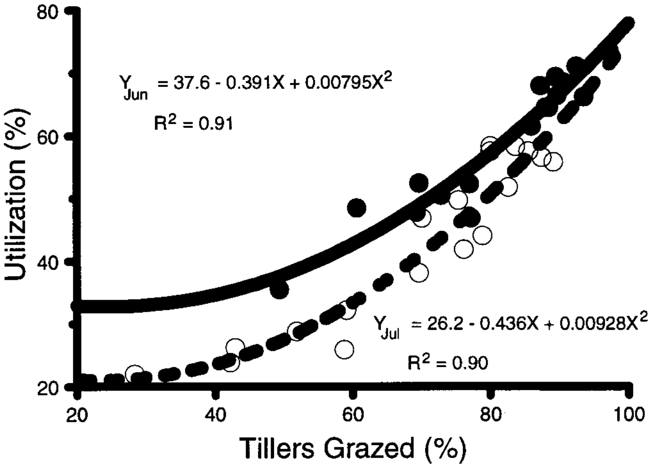

Fig. 3. Relationship between percentage of prairie sandreed tillers grazed and utilization of prairie sandreed in pastures at the Gudmundsen Sandhills Laboratory, near Whitman, Nebr., after grazing in mid-June (•) or mid-July (○) in 1995 and 1996.

Tiller Demography

Total end-of-season tiller recruitment averaged over stocking rates was about 10% higher after grazing in July compared to June in both years, 277 compared to 250 m^{-2} in 1995 and 211 compared to 193 m^{-2} in 1996. Availability of photosynthates for tiller development may have been higher in July because of a 30-day delay in grazing and consistently less use of prairie sandreed in July than in June (Cullan 1998). Mean tiller recruitment for grazed pastures was about 30% greater in 1995 (264 m^{-2}) compared to 1996 (202 m^{-2}) and 40% greater in control pastures in 1995 (278 m^{-2}) than in 1996 (198 m^{-2}). Differences in recruitment between years corresponded to 87% more precipitation from March to June in 1995 than in 1996 and concur with positive correlations between soil moisture and tiller recruitment for other species (Zhang and Romo 1995).

In 1995, increasing stocking rate from 16 to 48 AUD ha^{-1} in June reduced tiller recruitment whereas increasing stocking rate in July increased recruitment compared to ungrazed control pastures (Fig. 4). Measurable reductions in tiller recruitment occurred in June pastures when average use of prairie sandreed increased from 49% at 16 AUD ha^{-1} to 65% at 32 AUD ha^{-1}. Reductions in tiller recruitment were similar after moderate (32 AUD ha^{-1}) and heavy (48 AUD ha^{-1}) stocking rates because high grazing pressures resulted in near maximum utilization of 65 and 71%, respectively. Total end-of-season tiller recruitment in July pastures increased by about 21 m^{-2} for each 10 AUD ha^{-1} increase from 16 to 48 AUD ha^{-1}. This pattern corresponded to an increase in defoliation of about 9% for each 10 AUD ha^{-1} from 27% at 16 AUD ha^{-1} to 57% at 48 AUD ha^{-1}. Stocking rate effects on tiller recruitment in 1995 were not repeated or sustained in the following year, when average precipitation occurred, regardless of degree of use. Mullahey et al. (1991) reported similar findings at the same research location in a 3-year clipping study. We reject our hypothesis that recruitment of prairie sandreed tillers increases as cumulative grazing pressure increases and conclude that the effects of grazing on tiller recruitment in this species are inconsistent and limited by environmental variables.

It is unlikely that micro-environmental light conditions were different between years because grazing treatments produced a similar array of remaining herbage and foliar architecture each year (Volesky et al. 1999). Above-average precipitation and concurrently below average spring air temperatures may be important variables for recruitment of prairie sandreed tillers. Measurably higher prairie sandreed herbage in late spring 1995 compared to 1996 indicated that spring air temperatures did not limit

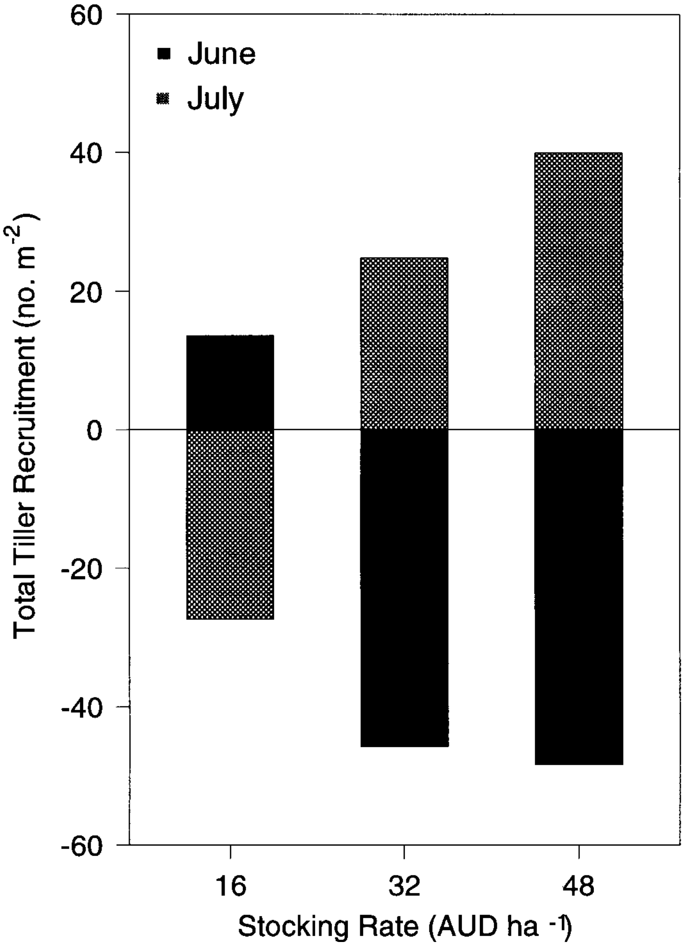

Fig. 4. Stocking rate effects on the difference (grazed-control) in total end-of-season recruitment of prairie sandreed tillers for pastures grazed in June (■) or (▨) July during 1995 compared to ungrazed control.

growth or that above-average precipitation allowed plants to compensate by mid-June in 1995. Larger differences in recruitment between years for control compared to grazed pastures may reflect differences in infiltration rates and/or depth and extent of roots. Heavy defoliation reduces root growth and nutrient uptake (Crider 1955, Engel et al. 1998). Tiller recruitment was reduced after grazing in June in both years when utilization exceeded 60% at 32 and 48 AUD ha^{-1} (Fig. 4). Consequently, we hypothesize that availability of soil moisture and ability of plants to absorb soil moisture appear to be the critical variables in prairie sandreed tiller recruitment.

Tiller mortality was generally less than 1% of the tiller population for all treatments in both years. Severely defoliated tillers remained green and succulent until killing frost, even when growing points were removed in July. In contrast to other species, reproductive growth in parental tillers had no effect on tiller mortality (Briske and Richards 1995). Mortality of prairie sandreed tillers occurred only when tillers were completely removed by grazing. Therefore, we reject our hypothesis that tiller mortality increases as cumulative grazing pressure increases and conclude that grazing pressure has no measurable effect on tiller mortality within years.

About 24% of the 1995 tiller populations in control pastures survived into the following growing season. These biennial tillers accounted for 33% of the 1996 tiller population. Tillers that had emerged and fully expanded 1 leaf blade by early June 1995 accounted for 82% of the biennial tillers in 1996 which is comparable to the year-to-year survival of northern wheatgrass *[Agropyron dasystachyum* (Hook.) Scribn.] tillers (Zhang and Romo 1995).

Management Implications

The high degree of correlation between percentage of prairie sandreed tillers grazed and utilization of prairie sandreed suggests that percentage of grazed tillers can be used to monitor early-summer use of this grass in the Nebraska Sandhills. Additional research is needed to develop efficient sampling procedures that can be used for monitoring and to determine if utilization of other species is related to use of prairie sandreed.

The effect of grazing on prairie sandreed tiller recruitment is limited by environmental variables. While soil moisture appears to be important, the specific variables and mechanisms have not been determined. Annual differences in this study indicate that increases in tiller density are inconsistent and may not be sustained in the following year. Managers can use equations in this paper and estimates of cumulative grazing pressure or percentage of grazed tillers as tools to achieve target levels of use of this species.

Relatively large increases in use per-unit-change of cumulative grazing pressure below 20 AUD Mg^{-1} indicate that cattle selectively graze prairie sandreed in June and July. Additionally, yield of current-year herbage in June may only be 20 to 50% of peak-standing crop when cattle are turned out in June, causing a 2 to 5-fold increase in cumulative grazing pressure. While grazing strategies would appear to have a limited effect on use of prairie sandreed, some strategies would produce predictably low or high cumulative grazing pressure in June or July. When grazing periods are < 2 months, initiating grazing in June at stocking rates recommended by the Natural Resources Conservation Service for 4 to 6-month summer grazing seasons, will result in relatively high early-summer grazing pressure and cause use of prairie sandreed to exceed 65% nearly every year. In contrast, stocking rangeland for near maximum average daily gains in cattle (Willms et al. 1986, Hart et al. 1988a, 1988b) under continuous season-long grazing for 4 to 6 months would result in relatively low monthly grazing pressures and nearly eliminate the potential for use of prairie sandreed to exceed 50% in June or July. Use of prairie sandreed should be monitored when the potential for high cumulative grazing pressure occurs in early summer.

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52:454–461 September 1999

Bison use of fire-managed remnant prairies

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Abstract

This study was designed to: 1) compare the landscape distribution patterns of bison on fire-managed prairie remnants in the tallgrass (Oklahoma), and mixed prairie (Nebraska); and 2) identify the extent to which fire and range site [topo-edaphic classification of the landscape] affect bison distribution patterns.

This research was conducted at 2 sites: the Niobrara Valley Preserve (1990–1996), and the Tallgrass Prairie Preserve (1993–1996). At both preserves, bison selected burned areas during the growing season for 1–3 years and mostly avoided old burns and unburned areas. There was an interaction between fire and range site in selection patterns. In the absence of fire, bison mostly avoided both the Choppy Sand range sites at the Niobrara Valley Preserve and Loamy Prairie range sites at the Tallgrass Prairie Preserve. When they were burned, however, these sites were highly selected. The main difference in bison selection patterns between the Tallgrass Prairie Preserve and the Niobrara Valley Preserve was observed during the dormant season. In the Tallgrass Prairie Preserve, burned sites continue to be preferred during the dormant period for an average of 2 years while in the Niobrara Valley Preserve selections were random. These differences can be explained by 2 mechanisms: the fall and winter re-growth of forage at the more southern latitude and the significant physiognomic changes that fire can cause in tall grass prairies. Our study documents a continuing interaction between the ecological processes of the fire regime and bison distribution and abundance within 2 of the major prairie landscapes of the Great Plains, and provides critical details for understanding this relationship.

Resumen

El objetivo de este estudio fue: 1) comparar el pastoreo de bisontes en pastizales nativos de Oklahoma y Nebraska manejados con fuego; y 2) determinar si el fuego influencia el uso de diversos “range sites” (range site es una combinacion nespecifica de topografia y suelos).

El experimento se condujo en dos lugares: la Niobrara Valley Preserve (1990–1996), y la Tall Grass Prairie Preserve (1993–1996). En ambos lugares, durante la epoca the crecimiento, los bisontes pastorearon de 1 a 3 años seguidos secciones recientemente quemadas y evitaron secciones no quemadas o quemadas mas the 3 años atras. La intensidad de uso fue influenciada por una interaccion entre el fuego y los range sites. Los bisontes pastorearon livianamente los Choppy Sand range sites en la Niobrara Valley Preserve y los Loamy Prairie range sites en la Tallgrass Prairie Preserve. Los mismos range sites, sin embargo, fueron intensamente pastoreados despues de la quema. Durante el otoño y el invierno los bisontes en la Tallgrass Prairie Preserve pastoreando intensament por 2 años seguidos las secciones quemadas, mientras que en la Niobrara Valley Preserve no se observaron diferencias en el uso de secciones quemadas y no quemadas. Esta disparidad se debio a: (a) la continuacion del crecimiento de los pastos en el otoño y parte del invierno en la Tallgrass Prairie Preserve; y (b) la alteracion que el fuego causo a la fisionomia de las praderas de la Tallgrass Prairie Preserve. Demostramos una interaccion entre el pastoreo de los bisontes y los procesos ecologicos generados por distintos regimenes de fuego y proveemos detalles tecnicos para el uso de fuego en estas praderas.

Key Words: Fire, grazing patterns, tallgrasss prairie, mixed prairie, range site.

Plains bison (*Bison bison bison*) were extirpated as a free-ranging species in the last 2 decades of the nineteenth century. The factors that influenced pre-historic bison distribution (Hanson 1984, McHugh 1972), and the distribution of their impacts on the biotic and abiotic environment (England and DeVos 1969, Malin 1953), thus, are generally unknown. Following the near extinction of bison, the Great Plains were developed for intensive agriculture, transportation corridors, and cities. Bison herds are once again expanding, although this time on prairie fragments within the developed landscape. These remnant prairies are critical to conserving biological diversity within the Great Plains (Samson and Knopf 1996). The interruption of landscape-scale processes, however, continues to be an overlooked mechanism reducing biodiversity (Leach and Givnish 1996). In commercial livestock operations neither large grazers nor fire are managed, for the most part, to preserve or restore ecological processes. Instead, they are managed to achieve individual species, or management unit objectives.

Research was funded by grants from The Nature Conservancy Ecosystem Research Program, USDA NRICGP 93-0051, and the National Science Foundation DEB-9627928.

Manuscript accepted 20 Oct. 1998.

Abiotic factors such as weather, topography, soils, and distance from water are suggested as the primary determinants of the large-scale distribution patterns of large herbivores (see review by Bailey et al. 1996). At smaller scales, the animal's spatial memory regarding factors such as forage composition, quantity and quality serve to improve foraging efficiency and define grazing patterns (Bailey et al. 1996). Biotic factors, therefore, should play a more significant role in defining bison distribution than abiotic ones within fragmented prairie remnants than on an unbounded prairie landscape. The modifications of many ecosystems processes (net primary production, nutrient cycling, etc.) by large grazers are widely recognized (Hobbs 1996). At moderate stocking rates, large grazers do not appear to influence, in the long term, plant species assemblages within plant communities, or alter the trajectory of plant succession at the landscape level (Jefferies et al. 1994, Biondini et al. 1998). Large grazers, however, have considerable short-term effects on vegetation at small scales. Examples include changes in bunchgrass size and tiller dynamics (Briske and Anderson 1990, Pfeiffer and Hartnett 1995), plant species diversity (Collins 1987, Hartnett et al. 1997), and plant above-ground biomass and live:dead ratio (Coppock et al. 1983, McNaughton 1984).

Great Plains land conversions and management have probably caused larger changes in landscape-scale processes than the replacement of bison grazing with cattle (*Bos taurus*) grazing (Hartnett et al. 1997). Yet, significant differences exist between the physiology, morphology, social behavior, and foraging ecology of bison and cattle which may make bison more adapted to some Great Plains grasslands (Christopherson et al. 1978, Peters and Slen 1964, Plumb and Dodd 1993, Towne et al. 1988). Bison select for the dominant perennial grasses forming the prairie matrix, show a strong preference for areas with young regrowth following fire and grazing, avoid wooded or broken topography during the breeding season, and spend relatively little time around water sources (Coppock and Detling 1986, Plumb and Dodd 1993, Shaw and Carter 1990, Steuter et al. 1995, Vinton and Hartnett 1992, Vinton et al. 1993, Coppedge et al. 1998).

Prairie preserves and native grassland pastures are relatively small considering the mobility of bison. Most of the abiotic factors associated with these prairie fragments (e.g. climate, weather, topography, soils) remained scaled similar to their original condition. The fire regime, however, can be re-scaled through the use of prescribed burning. Localized versions of the regional fire regime driven by a real-time fuel-forage interaction (Steuter et al. 1990) are implemented on several Great Plains preserves managed by The Nature Conservancy. Bison have been introduced as year-long, unsupplemented residents of these prairies.

The native rangelands of the mixed-grass and tallgrass prairie have been highly fragmented by farmland. Although the ecology of cattle grazing on prairie fragments has been studied intensively for 75 years [e.g Weaver and Clements 1938, Dyksterhuis 1949], there have been no opportunities, until recently, to study the ecology of bison grazing on relatively large mixed and tallgrass prairies managed with fire. During the last 20 years private bison ranches have developed throughout the central and eastern Great Plains. Many of these operations are based on native prairie remnants of high conservation value due to their rarity. Since bison offer previously unavailable management alternatives for these native prairie remnants, we have initiated studies to explore the contemporary response of these rangelands within the context of the evolutionary fire regime.

The objectives of this study were: 1) to compare the landscape distribution patterns of bison on fire-managed prairie remnants in the Tallgrass (Oklahoma), and Mixed prairie (Nebraska); and 2) to identify the extent to which fire and range site [topo-edaphic units of the landscape] affect bison distribution patterns. Results from this study should provide part of the framework for placing the aboriginal landscape-scale process of bison grazing within the context of contemporary prairie remnants.

Materials and Methods

Site Description

The research was conducted at 2 sites: the Niobrara Valley Preserve (1990–1996), and the Tallgrass Prairie Preserve (1993–1996). Both preserves are owned and managed by The Nature Conservancy. The Niobrara Valley Preserve is located in Brown, Cherry, and Keya Paha counties, Nebr. on the northern edge of the Sandhills (42° 46'N, 100° 00' W). The Sandhills are an extensive area of stabilized dunes dominated by bluestem (*Schizachyrium scoparium* Michx., *Andropogon gerardii* Vitman) and prairie sandreed (*Calamovilfa longifolia* Hook.) (Shiflet 1994). The Niobrara river and valley are significant features of the study site. The climate is continental with an average precipitation of 559 mm year^{-1}, and mean daily temperatures that range from –5.7°C in January to 24° C in July. The experiment was conducted in a 3,000 ha pasture established in 1988, with a bison stocking rate of 1.0 AUM ha^{-1} year^{-1}. An AUM is the amount of forage that a 454 kg bison consumes in 1 month (360 kg dry-wt., Heitschmidt and Taylor 1991). The bison pasture has 4 dominant range sites (Voightlander et al. 1992) (Table 1).

The Tallgrass Prairie Preserve is located in the northern half of the Osage Hills, Okla. (36° 50' N, 96° 25' W). The Osage Hills, an extension of the Flint Hills, are characterized by shallow to deep soils over limestone and limy shale (often exposed) and a well established drainage system. The study site is dominated by a bluestem prairie (Shiflet 1994) with savanna type vegetation occurring in the stream courses and in exposed bedrock areas. The climate is continental with an average precipitation of 877 mm year^{-1}, and average monthly temperatures that range from a low of –3.3° C in January to a high of 33.3° C in July . The study site was established in 1993 in a 1,970 ha pasture which was subsequently expanded to 2,575 ha in the Fall of 1995, and 2,875 ha in the Spring of 1996. The bison stocking rate, however, was kept constant at 1.2 AUM ha^{-1} year^{-1}. The bison pasture has 6 dominant range sites (Bourlier et al. 1979) (Table 2).

Fire Management

The study sites are managed with prescribed burning designed to mimic the seasonal distribution and return interval of fires for the pre-European settlement period (Steuter et al. 1990). Approximately 13% of the Niobrara Valley Preserve and 20% of the Tallgrass

Table 1. Niobrara Valley Preserve range site description, dominant vegetation, and estimated production.

Range Site	Area	Description	Dominant Vegetation	Estimated Production
	(%)			(kg ha^{-1})
Sand	35	Deep, well drained, coarse textured soils on level to gently rolling uplands	*Andropogon hallii, Panicum virgatum, Schizachyrium scoparium, Calamovilfa longifolia, Eragrostis trichodes,* and *Bouteloua hirsuta.*	2600
Choppy Sands	40	Deep well drained coarse textured soils on hilly uplands with stablized dunes	*Andropogon hallii, Panicum virgatum, Calamovilfa longifolia, Schizachyrium scoparium, Stipa comata, Eragrostis trichodes, Bouteloua hirsuta,* and *Muhlengbergia* pungens.	2400
Shallow to Gravel	20	Moderately fine to coarse textured soils underlain with gravel and coarse sand at depths 20cm to 50cm	*Bouteloua gracilis, Bouteloua hirsuta, Calamovilfa longifolia, Stipa comata, Andropogon hallii,* and *Schizachyrium scoparium*	1600
Sandy Savanna	5	Level to very steep areas on breaks or riparian areas characterized by grasslands interspersed by mature trees and brush	Grasslands interspersed with mature trees and brushes	Variable

Prairie Preserve pastures are burned each year to simulate the average fire-return interval of 7.5 and 5 years, respectively, estimated for the study sites in question (Wright and Bailey 1982). On both study sites, approximately 80% of the burns occur during the dormant season with the remainder taking place during the growing season to reflect seasonal differences in ignition sources, fuel conditions, fire intensity, and rates of fire spread (Higgins 1986, Cheney et al. 1993). Areas to be burned are selected from landscape units that meet a minimum size (>15 ha) using a weighted random procedure. The weighting factor is fine fuel accumulation immediately prior to burn date (the higher the fuel accumulation the higher the probability of selection). A minimum threshold for fine fuel capable of carrying a fire is set at 1,000 kg ha^{-1} as estimated from Forest Service models using local data (Burger and Rothermel 1984, Andrews 1986).

Bison Location

We recorded the landscape distribution of “mixed” bison groups which consist of adult females, juvenile

Table 2.. Tall Grass Prairie Preserve range site description, dominant vegetation, and estimated production.

Range Site	Area	Description	Dominant Vegetation	Estimated Production
	(%)			(kg ha^{-1})
Claypan	6	Level to gently sloping soils, fine to medium-textured topsoils, impervious subsoils within 50cm of the surface.	*Schizachyrium scoparium, Andropogon gerardii*, and *Panicum virgatum*	3000
Loamy Bottomland	5	Alluvial soils that are subject to flooding (riparian zones and overflow areas)	*Panicum virgatum, Sorghastrum nutans,* and *Andropogon gerardii* with mature trees and shrubs compromise 20% of the vegetation).	6100
Loamy Prairie	65	Upland soils more than 50 cm deep, with a loamy texture and permeable subsoils.	*Andropogon gerardii, Panicum virgatum, Sorghastrum nutans*, and *Schizachyrium scoparium*	5200
Shallow Savanna	5	Loamy upland soils that are less than 50 cm deep with exposed ledge rock and very shallow soils intermixed with deeper soils.	Mature trees and shrubs compromise 20% of the vegetation with *Schizachyrium scoparium* and *gerardii* as the dominant herbaceous species.	2100
Shallow prairie	16	Rocky and rough upland soils, less than 50 cm deep, slopes of less than 20%	*Schizachyrium scoparium, Bouteloua curtipendula, Andropogon gerardii, Sorghastrum nutans*, and *Panicum virgatum*.	2300
Sandy Savanna	3	Loamy or sandy texture upland soils more than 50 cm depth with gently to steep slopes.	*Schizachyrium scoparium, Andropogon gerardii,* and *Sorghastrum nutans.*	3300

females and males, and bulls generally younger than 4 years old. During the rut, older bulls were also part of these mixed groups. The location of bison groups within the pasture was determined throughout the year by regular (once or more per week) visual census conducted during the morning and afternoon. Determining the location of at least 90% of the bison herd was considered a minimum for a complete sample. Animal location was recorded with the use of USGS 7.5' topography series maps of the pasture overlain with a permanent 16 ha grid system. Total number of bison observed within each grid was aggregated on a 12 month basis to reflect growing season (April to October) or non growing season (November to March) distribution patterns.

The bison grid data, as well as the geographic location of prescribed burns and range sites were mapped onto 1:24000 USGS Quads and transferred to a Geographic Information System (GIS) using Erdas 8.1 (Erdas, Inc.). GIS layers corresponding to bison, fire, and range site locations were used to determine bison distribution patterns as a function of fire and range sites.

Statistical Analysis

The null hypothesis that bison select burned areas or range sites randomly and in proportion to their area was tested with the use of Chi square analysis (Manly 1993):

$$\chi^2_{(\alpha;NR-1df)} = \sum_{i=1}^{i=NR} \frac{(\mathbf{u}_i-\mathbf{u}_+\pi_i)^2}{\mathbf{u}_+\pi_i} \qquad \mathbf{(1)}$$

where NR= number of categories (burned sites by year, or range sites); u_i= the number of animals using resource i; u_+= total number of animals; π_i= proportion of resource i (proportion of burned or range site area i in the pasture). Interactions between burned area and range site selection were tested in a similar fashion with Chi square contingency tables (Mosteller and Rourke 1973). If either test was significant (null hypothesis rejected) we proceeded with the following analysis.

The 100(1-α)% multiple confidence interval for selection ratios was calculated as follows (Manly 1993):

$$CI(w_i) = \pm z_{\alpha/(2NR)}\sqrt{\frac{(1-\pi_i)}{u_+\pi_i}} \; where \; w_i = \frac{u_i}{u_+\pi_i} \qquad (2)$$

where $z_{\alpha/(2NR)}$ is the Bonferroni adjusted z value for the standard normal distribution; w_i= ratio between the proportion of bison using resource i and the one expected under the null hypothesis. Deviations of selection ratios from the null hypothesis ($w_i \neq 1$ with $P<\alpha$) were tested using a 1 df. Chi square analysis of the following form (Manly 1993):

$$\chi^2_{(\alpha/2NR-1));1df)} = \frac{(\mathbf{w}_i-\mathbf{1})^2\mathbf{u}_+\pi_i}{(\mathbf{1}-\pi_i)} \qquad \mathbf{(3)}$$

To test whether the selection of a given resource affects the use of other resources equation 3 was modified as follows:

$$\chi^2_{(\alpha/2NR-1));1df)} = \frac{(\mathbf{w}_{i/j=J}-\mathbf{1})^2(\mathbf{u}_+-J)\pi_{i/j=J}}{(\mathbf{1}-\pi_{i/j=J})} \qquad \mathbf{(4)}$$

where

$$\mathbf{w}_{i/j=J} = \frac{u_i}{(u_+-J)\,\pi_{i/j=J}}; \; \pi_{i/j=J} \; \frac{\pi_i}{\sum_{l=1,\,1\neq j}^{l=NR}\pi_l} \qquad (5)$$

where: (a) $\pi_{i/j=J}$ is the conditional probability of selecting any of the remaining NR-1 available resource (i=1,..,NR-1; i≠j) once resource j has been selected; and (b) $w_{i/j=J}$ is the ratio between the number of bison selecting resource i (i=1,..,NR-1; i≠j) and the one expected under a null hypothesis that incorporates the knowledge that J number of bison have already selected resource j (expected number of u_+-J bison selecting each of the remaining NR-1 resources). This analysis was used to determine: (a) whether the use by bison of current burns affects the selection of previous burns; and (b) whether fire restricts selection of range site and vice versa.

All reported differences are statistically significant at the 1% level unless otherwise stated.

Results

Niobrara Valley Preserve

Growing Season

Before prescribed burning treatments were applied (1990) selection of the landscape units that were eventually burned followed null model predictions ($[w_i-1]=0$) (Fig. 1). When treatments began, aggregate selection of burned areas (sum of all burned areas) by bison was higher than null model predictions from 1991 to 1995, but it declined from an average of 60% above model predictions for the 1991-1993 period to 30% in 1995 (Fig.1). By 1996, however, the

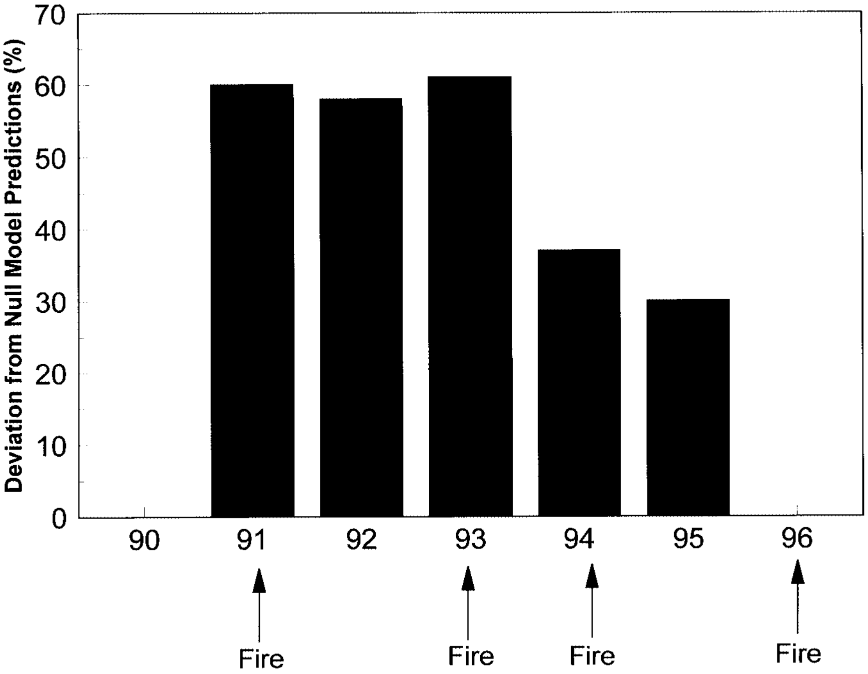

Fig. 1. Niobrara Valley Preserve. Aggregate bison selection of burned areas (sum of all burned areas) during the growing season. The bars represent significant departure (P<0.01) from null model predictions (bison use burned areas randomly and in proportion to their area)

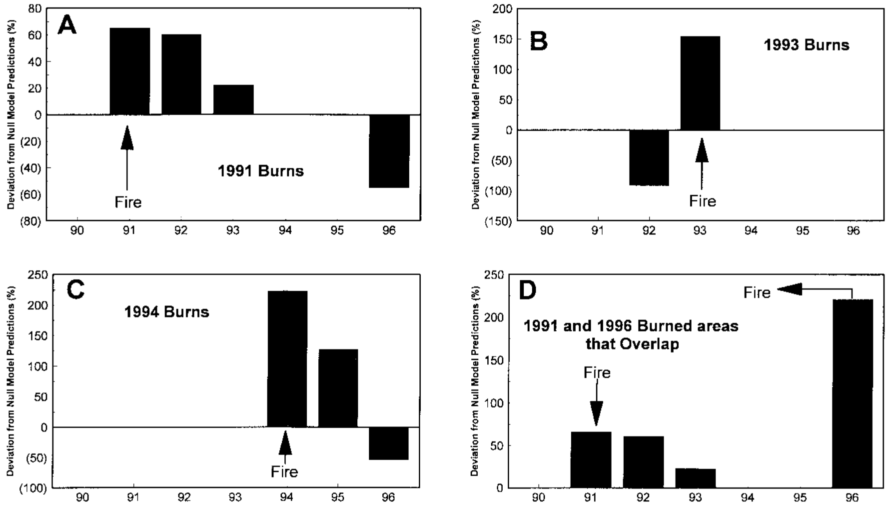

Fig. 2. Niobrara Valley Preserve. Bison selection of individual burn units during the growing season. The bars represent significant departure (P<0.01) from null model predictions (bison use burned areas randomly and in proportion to their area). (A) 1991 burns; (B) 1993 burns; (C) 1994 burns; (D) 1991 and 1996 burned areas that overlap.

aggregate selection of burned areas returned to null model predictions. The 1996 changes in selection patterns occurred because, for the first time, bison began to select new burns and avoid old ones (Fig. 2).

The 1991 burns were selected by bison for 3 consecutive years (Fig. 2), but avoided in 1996. The area burned in 1993 had been avoided by bison in 1992 but was highly selected when burned in 1993 (Fig. 2). Unlike the 1991 burn, however, the 1993 fire effect only lasted for 1 year primarily because of a switch in selection to the 1994 burn (Fig. 2). Selection of areas burned in 1994 had followed null model predictions from 1991 to 1993, but were substantially selected in 1994 and 1995. As with the 1991 burn, however, bison avoided this area in 1996. The fire of 1996 overlapped by 60% with the area burned in 1991 and was substantially (> 200% above null model predictions) selected by bison.

The Choppy Sands range site was mostly avoided by bison by (an average of 35% below null model predictions) from 1990 to 1993 but was highly selected in 1996 (Fig. 3). Sand range sites were selected above null model predictions only twice during the 7 years of the study.

The 1996 selection of the Choppy Sands reflects the capacity of fire to override range site effects since 93% of the 1996 burns occurred over this range site (Fig. 4). Fig. 4 shows the bison selection ratios of Choppy Sands contingent upon the selection of burned areas within it. Burned areas within the Choppy Sands were consistently selected by bison overriding the overall avoidance of the site when unburned (Fig. 3). When the effect of burning was taken out of bison selection patterns, Choppy Sands were either consistently avoided or followed null model predictions. The 1996 results are a clear example of fire dominating range site effects. As shown in Fig. 3, bison in 1996 substantially selected Choppy Sands, but when the fire effect is taken out of their selection patterns, there is no selection for Choppy Sands (Fig. 4).

Non-Growing Season

Bison selection patterns during the non-growing season were markedly different from the ones observed during the growing season. There was no significant effect of fire upon selection patterns for the entire 7 year period. Choppy Sands were avoided only 2 out of the 7 years, while Sands were selected above null model predictions only once during the same period of time (Fig. 3).

Tallgrass Prairie Preserve

Growing Season

Contrary to the selection patterns observed at the Niobrara Valley Preserve, there was not an aggregate selection of burned areas (sum of all burned areas) early in the study period. This result is probably due to the fact that while forage production in the Tallgrass Prairie Preserve was twice that of the Niobrara Valley Preserve, the

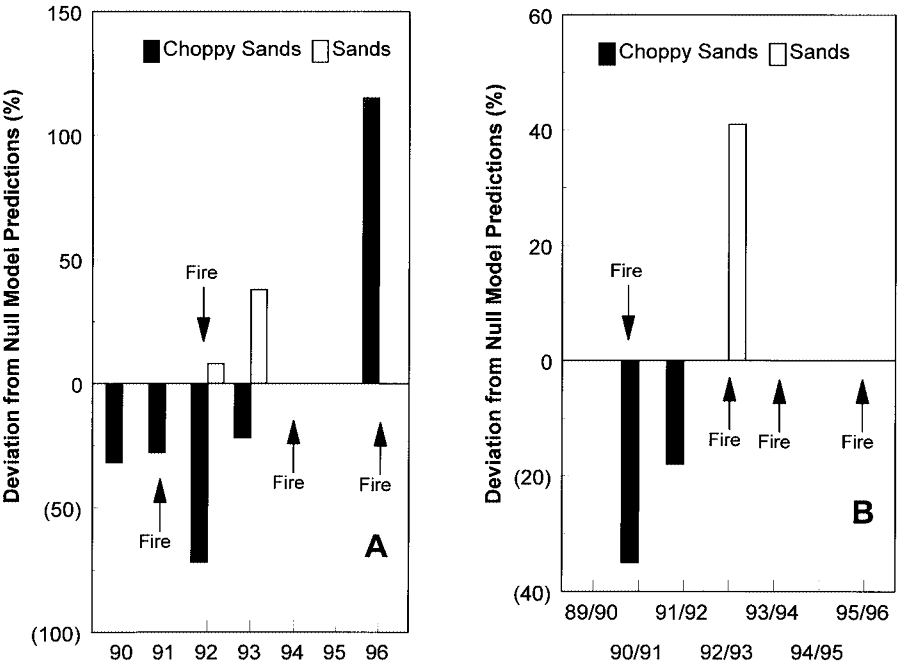

Fig. 3. Niobrara Valley Preserve. Bison selection of Sands and Choppy Sand range sites for both the growing and non-growing season. The bars represent significant departure (P<0.01) from null model predictions (bison use range sites randomly and in proportion to their area). (A) Growing season; (b) Non-growing season.

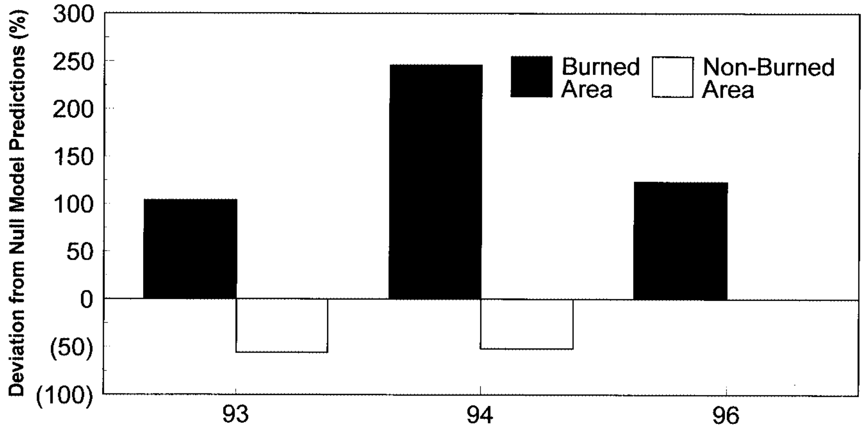

Fig. 4. Niobrara Valley Preserve. Bison selection of Choppy Sands range sites as affected by fire. The bars represent significant departure (P<0.01) from the conditional null model predictions as estimated by equation 4.

bison stocking rate was only 20% higher. Selection of burned areas at the Tallgrass Prairie Preserve was high (> 200%), but it was restricted to the most recent burns (Fig. 5a-c). As in the case of year 6 at the Niobrara Valley Preserve there was a significant avoidance of old burns as well as non-burned areas (Fig. 5a-c).

The only interaction between range sites and fire was observed on the Loamy Prairie range site (Fig. 5d). Use of Loamy Prairie followed the pattern of the overall landscape, which is not unexpected since this site represents 65% of the pasture. Use of this range site as a whole follows null model predictions (w=1) in all growing seasons. But, the results again showed the ability of fire to override range site effects: the burned area was highly selected (>150%) in 1994 and 1995 while the unburned areas were mostly avoided (40% reduction from null model predictions) (Fig. 5d).

Non Growing Season

Non-growing season response to fire was similar to that observed in the growing season, but lasted for 2 years rather than 1 and departures from null model predictions were on average 60% lower (Fig. 5a-d). These patterns were substantially different from those observed at the Niobrara Valley Preserve where there was no response to fire during the non growing season. A similar pattern was observed vis a vis range site. Again the only significant interaction was observed on the Loamy Prairie where the burned areas were highly selected, while the unburned ones were either avoided (≈ 25% below null model predictions), or followed null model predictions (Fig. 5d). As in the case of fire, the response was on average 60% lower than in the growing season.

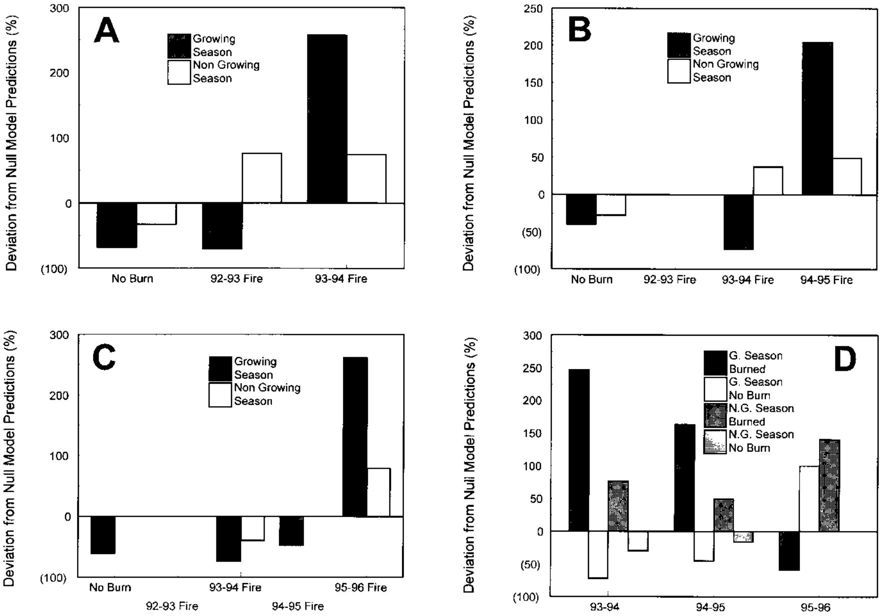

Fig. 5. Tall Grass Prairie. Selection of individual burn units and the Loamy Prairie range site for both the growing and non-growing season. The bars for the individual burn units represent significant departure (P<0.01) from null model predictions (bison select burned areas randomly and in proportion to their area). For the Loamy prairie site the bars represent significant departure (P<0.01) from the conditional null model predictions as estimated by equation 4. (A) 1993–1994 Bison selection patterns by fire; (B) 1994–1995 Bison selection patterns by fire; (C) 1995–1996 Bison selection patterns by fire; (D) Bison selection of Loamy Prairie Range site as constrained by fire.

Discussion

The strong attraction of bison to newly burned areas has been documented by others in western and more wooded mixed prairie areas (Coppock and Detling 1986, Shaw and Carter 1990). These studies described bison response to unique fire events largely as a response to a patch of high quality forage. Steuter et al. (1990) theorized that in the mixed prairie, bison selection of burned areas should last for 2 to 3 years and should be limited to the growing season. The hypothesis was based on the known effects of fire on annual forage production and seasonal forage quality.

Various studies have demonstrated the link between forage quality and fire (Britton and Steuter 1983, Ohr and Bragg 1985, Coppock and Detling 1986). The increase in forage quality after fire can be prolonged by grazing, since long term studies have shown a substantial increase in forage crude protein and digestibility as a result of moderate grazing (Milchunas et al. 1995). Along with improvements in forage quality, fire also increases above-ground plant production, in particular on tallgrass sites burned with intermediate frequency (4-10 year interval) (Seastedt et al. 1991, Ojima et al. 1994). Fryxell (1991) integrated the spatial components of forage quality and productivity with the grazing behavior of large herbivores by hypothesizing a direct link between herbivore aggregation and a substantial spatial variability in forage quality or production. Our experiments replicated the model assumptions of Fryxell (1991) by creating a complex spatial and temporal mosaic of unburned and burned patches within a large landscape. Results at both sites support Fryxell's (1991) predictions by showing a consistent spatial aggregation of bison in recently burned areas.

The temporal differences that we observed between the Niobrara Valley Preserve and the Tallgrass Prairie Preserve in the selection of burned areas highlight the significance of the forage production - bison stocking rate - season of burn interaction on landscape heterogeneity. Although the stocking rate on the Tallgrass Prairie Preserve is 0.2 AUM higher than on the Niobrara Valley Preserve (1.2 vs. 1.0 AUM ha^{-1} $year^{-1}$), forage production is on average 2 times higher (4,420 kg ha^{-1} vs. 2,200 kg ha^{-1}). Also, the average fire-return interval on Tallgrass Prairie Preserve is 5 years, while on the Niobrara Valley Preserve it is 7.5 years. This results in a 7% larger acreage, with twice the post-fire regrowth, available to bison on the Tallgrass Prairie Preserve. At the bison stocking rate used on the Tallgrass Prairie Preserve, forage regrowth following fire is more slowly and less completely removed by grazing and it matures more rapidly. This leads to a steeper decline in forage quality on newly burned areas of the Tallgrass Prairie Preserve when compared to the Niobrara Valley Preserve (Tieszen et al. 1998).

The attraction of bison to recently burned sites during the dormant season on the Tallgrass Prairie Preserve, but not on the Niobrara Valley Preserve, is likely explained by 2 mechanisms: the fall and winter regrowth of forage at the more southern latitude and the significant physiognomic changes that fire can cause in tallgrass prairies. Although warm season [C_4] grasses dominate both sites, temperatures following late summer and fall burns are more conducive to forage regrowth on the Tallgrass Prairie Preserve. A significant portion of this regrowth consists of cool season [C_3] grasses and sedges (Coppedge 1996, Coppedge et al. 1998). Late summer burns on the Niobrara Valley Preserve do not regrow sufficiently to attract bison during the winter (Pfeiffer and Steuter 1994). On the Niobrara Valley Preserve spring burns have been grazed more intensively during the previous summer, or have a mature forage quality more similar to unburned areas.

Collins (1987,1992) showed a substantial decline in plant community spatial heterogeneity coupled with an increase in the grass component with fire in tallgrass prairies. This physiognomic change should attract bison, since they prefer to graze large, un-fragmented, and relatively uniform plant communities that are dominated by grasses (Vinton and Harnett 1992, Plumb and Dodd 1993, Vinton et al. 1993, Steuter et al. 1995). The subsequent bison grazing forms a unique landscape patch in which rhizomatus grasses are favored over bunchgrasses (Pfeiffer and Steuter 1994, Pfeifer and Hartnett 1995), and forb composition and density changes as a function of season of burn.

Pre-fire results from the Niobrara Valley Preserve suggested that range site would have a significant effect on bison selection of burned areas (Steuter et al. 1995). It now appears that in both the tallgrass and mixed-grass prairies, fire can override range site effects. This allows for a more even, or more clumped, distribution of bison use across the landscape depending on the specifics of the fire regime.

Our results suggest that the details of the fire regime, and bison distribution and abundance within the tallgrass and mixed prairie have a substantial effect on the spatial and temporal distribution of habitat patches. These details were largely controlled by a sequence of Plains Indian cultures during the Holocene (Hanson 1984, Higgins 1986). For example, although Shaw and Lee (1997) report little bison use of the southern Tallgrass prairie from 1806 to 1857, summer burning by earlier Tallgrass prairie inhabitants may have greatly increased winter bison use of this prairie type. Our results re-enforce the notion that human management of the fire regime and large grazers was a basic, but not necessarily static, component of Great Plains grasslands.

Management Implications

Our research provides detail on how fire determines the distribution of grazing by bison within tallgrass prairie and mixed prairie, in the Great Plains. The powerful attraction of bison to burned patches within large heterogeneous landscapes may be used to achieve several management objectives. Since the bison-fire management regime results in between-year rotations of grazing and rest, rather than within-season rotations of grazing deferment, there are larger, longer and possibly more useful contrasts in standing crop on different parts of the landscape for other wildlife species to use. For example, species preferring high residual cover for nesting [waterfowl and Henslow's Sparrow (*Ammodramus henslowii*)] would be undisturbed in areas unburned and avoided by bison for several years. Species preferring short stature grassland for nesting, feeding, or lekking [Upland Sandpiper (*Bartramia longicuada*), Chestnut-collared Longspur (*Calcarius ornatus*), Greater Prairie Chicken (*Tympanuchus cupido*)] would be able to select recently burned and intensively grazed areas. In addition, forb-rich "food plots" are created by intensive bison grazing and wallowing of late summer burn patches, which experience a short-term increase in low succession plants such as *Ambrosia spp.* In general, the almost exclusive grazing of graminoids that has been documented for bison should lead to an increase in forb diversity and abundance.

The new growth from prescribed burns could be used to draw bison away from grazing sensitive resources, or attract them to accessible viewing, round up, or harvest areas [an ages-old idea]. Areas burned to control woody plants, and selected by bison during the spring shed of their winter coats, would have additional small tree kill due to rubbing and horning.

Furthermore, the early growth of these burned areas should improve bison quality for lactation and subsequent conception rates following winter nutrient stress. Fall and winter forage quality could be improved by late summer burns in the southern tallgrass prairie, thus improving bison winter condition without supplemental feeding. With the proper stocking rate and fire regime, planned grazing might be distributed with much lower investment in cross-fencing. Less cross-fencing may result in a more dynamic spatial and temporal expression of plant communities.

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52:462–470 September 1999

Livestock response to multispecies and deferred-rotation grazing on forested rangeland

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Abstract

Performance of cow-calf (*Bos taurus*) and ewe-lamb (*Ovis aries*) units was compared under multispecies versus single-species grazing and deferred-rotation versus continuous stocking during a 10-year grazing trial. Treatments were arranged in a 3 species (cattle, sheep, or both species) by 2 grazing method (deferred rotation or continuous) factorial using a randomized-complete block design with 2 blocks. All animals were individually weighed at initiation, mid-point, and termination of each grazing season. Livestock species and grazing method did not interact for any dependent variable ($P>0.05$). Average daily gain (ADG) was greater ($P<0.05$) when calves were alone than when mixed with sheep (1.04 vs 1.01 kg day^{-1}, respectively), but ADG of lambs was greater ($P<0.05$) when mixed with cattle than alone (0.25 vs 0.23 kg day^{-1}, respectively). Cow and ewe ADG were unaffected ($P>0.05$) by animal species mixture. Production of progeny (gain of calves and lambs) and total production (gain of progeny and dams) per ha was greater ($P<0.05$) using sheep or mixed species than cattle (17.8, 17.8, and 11.2 kg ha^{-1} respectively, for progeny, and 22.4, 24.5, and 17.6 kg ha^{-1} respectively, for total). Calves grew faster ($P<0.05$) under continuous than deferred-rotation grazing (1.04 vs 1.01 kg day^{-1}). Ewes gained more rapidly ($P<0.05$) during the second half of the grazing season under deferred-rotation than continuous grazing (0.049 vs 0.023 kg day^{-1}). Multispecies or sheep grazing appeared more appropriate than cattle for this environment. Deferred-rotation grazing appeared superior for sheep performance, but continuous grazing allowed greater calf performance.

Key Words: common grazing, mixed species grazing, dual grazing, livestock performance, grazing systems, grazing methods

Resumen

En un ensayo de 10 años de duración, se comparó el comportamiento de unidades de vaca-becerro (*Bos taurus*) y oveja-cordero (*Ovis aries*) apacentando en forma combinada e individual en los sistemas de apacentamiento de rotacional diferido y continuo. Los tratamientos se evaluaron bajo un diseño experimental de bloques completos al azar en arreglo factorial de 3 especies (bovinos, ovinos o ambas especies) y 2 métodos de apacentamiento (rotacional diferido y continuo). Todos los animales se pesaron individualmente al inicio, mediados y fin de cada estación de apacentamiento. La especie de ganado y el método de apacentamiento no interactuaron con ninguna de las variables dependientes ($P>0.05$). La ganancia diaria promedio de peso (GDP) fue mayor ($P<0.05$) cuando los becerros apacentaron solos que mezclados con borregos (1.04 vs 1.01 kg day^{-1}), en contraste la GDP de los corderos fue mayor ($P<0.05$)cuando apacentaron mezclados con bovinos que cuando lo hicieron solos (0.25 vs 0.23 kg day^{-1}). La GDP de vacas y ovejas no fue afectada ($P>0.05$) por la mezcla de especies animal. La producción de la progenie (ganancia de becerros y corderos) y la producción total (ganancia de la progenie y madres) por hectárea fue mayor ($P<0.05$) utilizando ovinos o especies combinadas que apacentando solo bovinos (17.8, 17.8 y 11.2 kg ha^{-1} respectivamente para la progenie y 22.4, 24.5 y 17.6 kg ha^{-1} para la producción total). Los becerros crecieron más rápido ($P<0.05$) en el sistema de apacentamiento continuo que en el rotacional diferido (1.04 vs 1.01 kg day^{-1}). Durante la segunda mitad de la estación de apacentamiento, las ovejas ganaron peso más rápidamente ($P<0.05$) en el sistema rotacional diferido que en el continuo (0.049 vs 0.023 kg day^{-1}). Para este ambiente, el uso de ovinos o especies combinadas parece ser más apropiado que el uso de bovinos. El sistema rotacional diferido parece ser superior para el comportamiento de ovinos; sin embrago, el apacentamiento continuo permitió un mejor comportamiento productivo de los becerros.

Concurrent grazing with more than 1 species of animal is expected to improve animal performance, carrying capacity, and range condition and productivity (Nolan and Connolly 1997, Walker 1994, 1997). These benefits are expected to be greatest on diverse landscapes, such as rangelands, where animal specific differences in diet selection and grazing distribution can be exploited to obtain more uniform utilization of the entire resource (Baker and Byington 1986). Most grazing trials to evaluate livestock responses to multispecies grazing have been done on improved pastures (e.g. Bennett et al.

This research was supported by the Utah Agricultural Experiment Station, Utah State University, Logan, UT 84322-4810. Approved as Journal Paper No. 6005.

The authors acknowledge the contributions of former principal investigators involved throughout the life of this project who allowed such long-term research to be possible, including Darrell Matthews, Warren Foote, and Gary Snowder.

Manuscript accepted 11 Nov. 1998.

1970, Nolan and Connolly 1989, Abaye et al. 1994), with the only U.S. rangeland studies conducted in Texas (Merrill and Young 1954, Merrill et al. 1966, Taylor 1985).

Grazing experiments to evaluate livestock responses to deferred-rotation have been more common. Literature reviews of animal responses to grazing methods (e.g. Driscoll 1967, Pieper 1980) indicated that specialized grazing methods, including deferred-rotation and others, have decreased or had no effect on animal performance in the majority of studies, with relatively few instances of a specialized grazing method improving animal performance.

A study was conducted from 1980 through 1990 to evaluate performance of sheep and cattle when grazed together or separate under continuous stocking or deferred-rotation grazing on high-elevation summer range. Matthews et al. (1986) published livestock data from early years of this study. Results concerning a second objective to evaluate vegetation responses will be published separately.

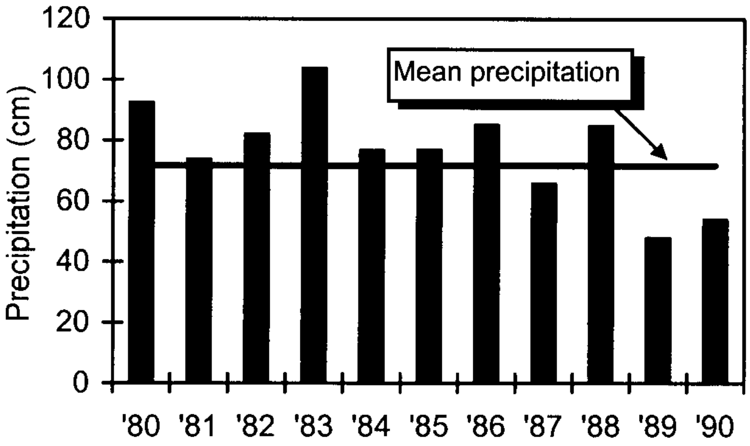

Fig. 1. Annual precipitation during each year of the study period and long-term mean precipitation (1970–1992).

Materials and Methods

Study Site

The study was conducted at a Utah Agricultural Experiment Station (UAES) research site located about 43 km southeast of Cedar City, Ut. (about 37°30' North latitude, 113° West longitude). The site consisted of about 1,310 ha of privately owned rangeland leased by UAES. The mean elevation of the site was about 2,600 m, and ranged from 2,300 to 2,900 m. The site had a typical montane physiography. The vegetation was a mosaic of forested and open plant communities. The overstory of the forested areas was quaking aspen (*Populus tremuloides* Michx.) or Gambel's oak (*Quercus gambelii* Nutt.). The herbaceous vegetation was dominated by grasses, primarily Letterman's needlegrass [*Achnatherum lettermanii* (Vasey) Barkworth], Kentucky bluegrass (*Poa pratensis* L.), slender wheatgrass [*Elymus trachycaulus* ssp. *trachycaulus* (Link) Gould ex Shinners], and mountain brome (*Bromus marginatus* Nees ex Steud.). The most common forbs were American vetch (*Vicia americana* Muhl. ex Willd.) and mountain tarweed (*Madia glomerata* Hook.). The most prevalent shrub was mountain snowberry (*Symphoricarpos oreophilus* var. *oreophilus* Gray). Bowns and Bagley (1986) indicated potential natural vegetation for this area should be dominated by tall forbs, but historical, heavy sheep grazing has caused the shift to grass dominance.

Precipitation records have been maintained from 1970 to present at a similar elevation about 10 km north of the study site (Fig. 1). The precipitation pattern is bimodal, with peaks during winter as snow and late summer as thunderstorms. Precipitation was above average during the first 7 years of the study, but below average during 3 of the final years. This allowed the opportunity to observe responses during good and poor growing conditions.

Grazing Treatments

Mixed species grazing (cattle alone, or cattle-sheep mixed) and grazing method (season-long or deferred-rotation) were replicated twice in a randomized-complete block design using a 3 × 2 factorial arrangement. For mixed-species grazing, 5 ewes with progeny were substituted for 1 cow-calf pair, which is the most commonly accepted replacement ratio, and is based on relative differences in forage consumption (Walker 1994). Deferred-rotation grazing used 2 paddocks, with rotation at about the middle of the grazing season. The paddock grazed initially was alternated in consecutive years. Considering that deferred-rotation required 2 paddocks per experimental unit, the study site was fenced into 18 individual paddocks of about 73 ha each. Paddock size ranged from 57 to 87 ha. Thus, each experimental unit of deferred-rotation was about twice the size of each experimental unit of continuous stocking, but the area occupied by livestock at any point in time was similar. One pond was excavated in each paddock to provide livestock water. The blocking factor was visual similarity of paddocks based on physiographic and vegetative characteristics described above. Paddocks were assigned randomly to treatment within block except 1 paddock containing tall larkspur [*Delphinium barbeyi* (Huth) Huth] was purposefully assigned sheep only to avoid poisoning cattle.

Stocking rate was set in the initial year based on historical stocking rates on the study site and was subsequently adjusted annually at the beginning of the grazing season in each experimental unit based on previous year's utilization and amount of winter precipitation received before initiation of grazing. Utilization was visually estimated at the end of each grazing season based on relative uniformity of remaining herbage among experimental units. Thus, stocking rate was adjusted in each experimental unit based on differences in previous year use and expected forage abundance to achieve targeted use of about 50 to 55%.

Cooperating producers provided livestock. The same cow herd was used throughout the study. Cattle breeds included Herefords and crosses of other breeds, primarily Angus and Simmental, on Herefords. Calves were born in February and March throughout the study, and weaned after the livestock were removed from the study site each year. The sheep used from 1980 through 1984 were from the Utah State University (USU) research flock located at Southern Utah University in Cedar City. This flock was sold in 1984. Sheep were provided in remaining years by a local producer that bought a large portion of the USU flock, allowing many of the same sheep to remain in their treatments through this transition. Sheep breeds in both flocks were straightbreds or crosses of Targhee, Suffolk, Rambouillet, and Finn. Lambs were born in April and were weaned in mid-September throughout the study. Individual cows and ewes were permanently assigned to treatment groups so they returned to the same experimental unit each year. Cows and ewes were stratified to treatment groups at initiation of the experiment by breed and age. Animal weight and rate of lambing among ewes were not used to stratify individuals to treatment because they were unknown at the time of assignment. The number of cows and ewes used each year varied based on stocking rate adjustments (Table 1). New animals needed when stocking rates were increased or replacements for culled individuals were similar to the existing livestock in age and breed composition. Cows and ewes that did not have progeny at the beginning of each grazing season were replaced with a contemporary with progeny. Lambing rates and initial weights of livestock varied among years (Table 1). All livestock resided on sagebrush (*Artemisia* spp. L.) dominated desert rangeland or farmland when not grazing the study site, as is typical for migration among seasonal grazing resources in this region.

Data Collection

All animals (cows, calves, ewes, and lambs) were individually weighed at initiation and termination of the grazing trial in mid-June and mid-September, respectively, of each year. Actual dates varied yearly based on range readiness for initiation and marketing of lambs for termination. Cattle and ewes remained on the study site for about 2 weeks after final weighing each year, but final weights had to be recorded before lambs were removed to be marketed. All animals were also weighed individually at midseason in all years when rotation occurred in the deferred-rotation treatment. Data from 1989 are not used herein because reliable weight data were not collected that year. Weights were used to calculate average daily gain (ADG, kg day^{-1}) for each half and the entire grazing season for each class of livestock (calves, cows, lambs, ewes) and gain per ha (kg ha^{-1}). Gain per ha was calculated over the entire season for progeny only, dams only, and total (progeny and dams combined). Production per ha of progeny only represents salable product to evaluate economically important productivity from each system, while production per ha of dams only and dams with progeny contributes to depiction of total biological productivity.

Table 1. Total number of cows and ewes assigned to treatments, mean number of lambs per ewe, and initial body weights of each class of livestock during each year.

				Initial weight			
Year	Cows	Ewes	Lamb rate	Calves	Cows	Lambs	Ewes
	- - - - - -(No.) - - - -			- - - - - - - - - - - - - (kg) - - - - - - - - - - - - - -			
1980	127	669	1.66	133.0	409.9	22.6	64.0
1981	144	738	1.67	123.4	407.4	18.9	61.1
1982	153	793	1.54	126.1	417.6	18.8	61.9
1983	161	801	1.55	126.1	415.9	22.0	60.5
1984	172	867	1.60	126.0	487.0	18.6	62.5
1985	177	880	1.54	128.4	477.9	22.8	67.0
1986	171	943	1.56	164.6	510.0	20.8	63.9
1987	168	838	1.61	148.4	491.2	25.3	70.7
1988	172	905	1.59	141.1	505.0	25.4	67.9
1990	120	646	1.53	118.4	538.6	25.6	67.1

Data Analysis

Analysis of variance was conducted using a randomized-complete block design with a split-plot treatment structure. The 3 × 2 factorial of livetock species × grazing method and their interaction was the main plot, using the combination of block × species, block × grazing method, plus block × species × grazing method as the error term. Year and its 2- and 3-way interactions with main plot effects were in the sub-plot, with the residual as the error term. This model was initially used to evaluate lambing rate and livestock weight at initiation of each grazing season because these were variables that could not be controlled for. Lambing rate did not respond to treatments or interactions ($P\geq0.55$), but did vary among years ($P=0.06$). Lambing rate was not used as a covariate because this variation would be absorbed into the year effect. Initial weight varied ($P=0.0001$) among years for all classes of livestock, and sometimes varied among treatments ($P<0.10$). Therefore, initial weight was incorporated into the model as a covariate.

When F tests were significant within the main plot, least squares means were separated using LSD. Split-plot appropriate standard errors for least squares means and LSD for significant interactions were calculated according to Cochran and Cox (1957). When F tests were significant in the subplot, linear and quadratic contrasts were constructed to evaluate trends across years. Higher level polynomial contrasts could have been constructed, but were considered of little value in interpreting the data. Significance was interpreted at $P\leq0.05$ for all tests unless otherwise indicated.

Results and Discussion

Animal species and grazing method did not interact ($P>0.05$) for any dependent variable, so each of these main effects are discussed separately. Additionaly, year × animal species × grazing method was never significant ($P>0.05$).

Livestock Performance

Treatment Effects. Calf average daily gain (ADG) was greater ($P=0.03$) over the entire grazing season when grazed alone rather than with sheep, although differences were small (Table 2). This difference was due primarily to higher ($P=0.09$) ADG during the first half of the grazing season followed by similar ($P=0.49$) ADG during the second half of the grazing season. This resulted in greater mid-season ($P=0.05$) and final ($P=0.01$) calf weights when grazed

Table 2. Mean livestock average daily gain (ADG, kg day^{-1}) response in multispecies or deferred-rotation grazing.

	Livestock species			Grazing method		
Item	Cattle only	Multi-species	Sheep only	Season-long	Deferred-rotation	SE[1]
	- (kg day^{-1}) -					
	Calf ADG					
First half[2]	1.10^{d}	1.05^{c}	—	1.09	1.05	.028
Second half[2]	.99	.97	—	1.00	.97	.038
Total[2]	1.04^{b}	1.01^{a}	—	1.04^{b}	1.01^{a}	.013
	Cow ADG					
First half	.87	.91	—	.94	.84	.101
Second half	.34	.31	—	.28	.36	.084
Total	.59	.59	—	.59	.58	.030
	Lamb ADG					
First half	—	.34^{b}	.32^{a}	.34	.33	.005
Second half	—	.15^{b}	.14^{a}	.14	.14	.004
Total	—	.25^{b}	.23^{a}	.24	.24	.003
	Ewe ADG					
First half	—	.15^{b}	.12^{a}	.14	.13	.015
Second half	—	.04	.04	.02^{a}	.05^{b}	.006
Total	—	.09^{d}	.08^{c}	.08	.09	.008

[1] SE = Standard error.

[2] First half, second half, and total refer to portions of the grazing period.

[a,b] Within a row and ANOVA effect, means lacking a common superscript letter differ ($P<0.05$).

[c,d] Within a row and ANOVA effect, means lacking a common superscript letter differ ($P<0.10$).

alone (Table 3). Cow ADG and weight (Tables 2 and 3) did not respond to species mixture (P>0.65). Lamb ADG (Table 2) was greater when mixed with cattle than alone during all periods (P=0.005, 0.02, and 0.001 for first half, second half, and total season, respectively). This resulted in lambs grazed with cattle being heavier at both mid-season (P=0.003) and final (P=0.001) weigh dates (Table 3). Total season ewe ADG was greater (P=0.08) when mixed with cattle because the ewes with cattle gained more rapidly (P=0.04) during the first half of the season followed by similar (P=0.66) ADG during the second half (Table 2). Ewe weights were greater at both the mid-season (P=0.04) and final (P=0.04) weigh dates when mixed with cattle (Table 3). The difference in performance response by sheep and cattle may be because of historical sheep grazing on the study site that had shifted the plant community from forb to grass dominance, particularly Letterman's needlegrass (Bowns and Bagley 1986), that was avoided by sheep but relatively preferred by cattle. Thus, the decrease in sheep numbers relative to cattle resulted in decreased competition for less abundant forage desired by sheep. This allowed the sheep mixed with cattle to graze more selectively for their desired vegetation and, thus, receive a more nutritious diet, resulting in greater performance. Relative abundance of forage desired by cattle was much greater, so ability to select a more nutritious diet was not as greatly influenced by animal species mixture. The difference in performance by cattle was a 0.03 kg day^{-1} improvement in calf total-season ADG when grazed without sheep. This small difference does not appear to be biologically important, despite its statistical significance. These results also agree with the literature, in that sheep performance usually increased when mixed with cattle, but cattle responses have been mixed, and usually smaller in magnitude than sheep responses (Nolan and Connolly 1997, Walker 1994, 1997). Walker (1994) also indicated that sheep appear to be more competitive than cattle when mixed because sheep are better able to select desired vegetation and can graze closer to the ground.

Grazing method did not influence calf average daily gain (ADG) (Table 2) during either half of the grazing season (P = 0.13 and 0.33 for first and second halves, respectively), but calves gained 0.03 kg day^{-1} more (P = 0.04) during the entire season under season-long than deferred-rotation grazing. This resulted in calves that weighed 2.3 (P=0.09) and 4.1 kg (P=0.007) more at the midpoint and end of the grazing season, respectively (Table 3). This small difference does not appear to be biologically important, despite its statistical significance. Cow ADG and weight (Tables 2 and 3) did not respond to grazing method (P>0.24). Lamb ADG did not respond (P>0.10) to grazing method during any period (Table 2). However, lamb mid-season weight (Table 3) was greater (P=0.07) under season-long grazing, but this difference disappeared (P=0.35) by market time (end of the grazing season). Ewe ADG (Table 2)

Table 3. Mean livestock weight (kg) response to multispecies or deferred-rotation grazing at the middle and end of the grazing season.

	Livestock species			Grazing method		
Item	Cattle only	Multi-species	Sheep only	Season-long	Deferred rotation	SE[1]
	- (kg) -					
	Calf weight					
Middle	186.5^{b}	183.8^{a}	—	186.3^{d}	184.0^{c}	1.2
Final	235.8^{b}	232.5^{a}	—	236.2^{b}	232.1^{a}	0.8
	Cow weight					
Middle	505.9	506.4	—	508.8	503.5	4.6
Final	523.5	523.0	—	524.2	522.2	3.2
	Lamb weight					
Middle	—	38.89^{b}	37.44^{a}	38.41^{d}	37.92^{c}	0.2
Final	—	45.51^{b}	43.37^{a}	44.48	44.29	0.2
	Ewe weight					
Middle	—	73.13^{b}	71.17^{a}	72.31	72.00	0.8
Final	—	75.18^{b}	73.33^{a}	73.74	74.77	0.8

[1] SE = Standard error.

[a,b] Within a row and ANOVA effect, means lacking a common superscript letter differ ($P<0.05$).

[c,d] Within a row and ANOVA effect, means lacking a common superscript letter differ ($P<0.10$).

Table 4. Mean response of livestock average daily gain (ADG) and production per ha to year effect.

	Year											Contrasts[1]	
Item	1980	1981	1982	1983	1984	1985	1986	1987	1988	1990	SE[2]	L	Q
					Calf ADG (kg day^{-1})								
First half[3]	.97	.98	1.05	1.37	.94	1.02	.73	1.28	1.28	1.11	.063	.01	.39
Second half	.88	.97	.89	1.01	.95	1.04	.95	1.07	1.05	1.03	.056	.005	.58
Total	.93	.97	.98	1.14	.94	1.03	.84	1.17	1.17	1.11	.038	.0001	.22
					Cow ADG (kg day^{-1})								
First half	.43	.40	.46	1.66	.48	.87	1.12	1.34	1.15	.96	.126	.09	.0003
Second half	.54	.53	.52	.77	.33	.36	.07	.35	.17	−.43	.108	.04	.0001
Total	.47	.45	.50	1.05	.41	.59	.59	.82	.67	.33	.055	.82	.0001
					Lamb ADG (kg day^{-1})								
First half	.657	.282	.305	.275	.268	.297	.322	.288	.330	.279	.008	.0001	.0001
Second half	.108	.096	.057	.160	.236	.203	.150	.173	.133	.119	.011	.07	.0001
Total	.261	.211	.228	.231	.254	.251	.232	.238	.239	.220	.006	.60	.36
					Ewe ADG (kg day^{-1})								
First half	.109	.107	.118	.131	.100	.141	.156	.173	.199	.119	.013	.003	.24
Second half	.062	−.015	.050	.060	.077	.067	.076	.022	−.029	−.012	.012	.01	.0001
Total	.089	.040	.081	.089	.088	.102	.113	.099	.088	.066	.006	.08	.0001
					Livestock production (kg ha^{-1})								
Progeny	11.7	15.2	14.8	13.9	18.7	18.1	17.3	16.8	17.0	12.2	.51	.0001	.0001
Dams	5.1	5.8	7.2	9.4	5.8	6.2	6.9	6.0	5.2	1.6	.48	.0001	.0001
Total	16.7	21.0	22.1	23.3	24.6	24.3	24.2	22.8	22.2	13.8	.83	.31	.0001

[1] Probability of greater F for linear (L) and quadratic (Q) polynomial contrasts.
[2] SE = Standard error
[3] First half, second half, and total refer to portions of the grazing period.

was similar (P=0.66) during the first half of the grazing season, but was over 2 times greater (P=0.008) under deferred-rotation grazing during the second half. Because ADG was much lower during the second than first half of the season, total-season ADG did not differ (P=0.18). Ewe weight (Table 3) did not differ at either date (P=0.63 and 0.17 for mid- and final weights, respectively). However, this does not diminish the value of the difference in late-season ADG. Improving nutritional status as evinced by increasing body weight immediately before the breeding season can be important to fertility in ewes (Dunn and Moss 1992). Instituting deferred-rotation grazing in a mixed-species system may benefit the sheep flock (ewe nutritional status at breeding) at the expense of the cattle herd (calf weaning weight). Depending on market conditions, this may be immaterial if both species are owned by the same producer, but could cause conflict if different producers own each species. Of 29 studies reviewed by Driscoll (1967), grazing methods such as deferred-rotation decreased (12), maintained (9), or increased (8) animal performance compared to continuous stocking. Pieper (1980) reviewed 24 studies, and reported that grazing method decreased (14), maintained (4), or increased (6) animal performance. Although there was some overlap of the studies in these 2 reviews, they indicate that grazing methods have no effect or are detrimental to livestock performance in the majority of cases. Many range scientists (Launchbaugh et al. 1978, Pieper 1980, Kothmann 1980, among others) have acknowledged that most specialized grazing methods have been developed to improve range vegetation characteristics with little concern for the effect on animals. Depending on the species of livestock chosen, this study provided mixed results, as well. The net effect, however, was that there was not a distinct advantage or disadvantage across both species of livestock.

Year Effects. Calf average daily gain (ADG) increased linearly ($P \leq 0.01$) across years during all weigh periods (Table 4). This response may typify genetic improvement in the cow herd over time. However, interactions indicated it was modified by treatments. Grazing method interacted with year for ADG during the second half of the season (P=0.01, Fig. 2). There was no trend across years under season-long grazing but a linear increase (P=0.0005) in ADG under deferred-rotation grazing. Apparently, calves performed more poorly under deferred-rotation in the early years but improved to be comparable to season-long grazing during the remainder of the study. Species (P=0.01) and grazing method (P=0.04) both interacted with year for total season ADG (Fig. 2). Calf ADG increased linearly both with and without sheep, but also tended to change quadratically without sheep. Average daily gain responded quadratically under season-long but linearly under deferred-rotation grazing. Differences in responses depicted by these interactions are relatively small

Table 5. Mean livestock weight (kg ha^{-1}) response by progeny, dams, and both to multispecies or deferred-rotation grazing.

	Livestock species			Grazing method		
Item	Cattle only	Multi-species	Sheep only	Season-long	Deferred rotation	SE[1]
			(kg day^{-1})			
Progeny	11.2^a	17.8^b	17.8^b	16.3	14.8	1.42
Dams	6.4^b	6.7^b	4.7^a	5.8	6.0	.58
Both	17.6^a	24.5^b	22.4^b	22.1	20.9	1.89

[1] SE = Standard error.
[a,b] Within a row and ANOVA effect, means lacking a common superscript letter differ (P<0.05).

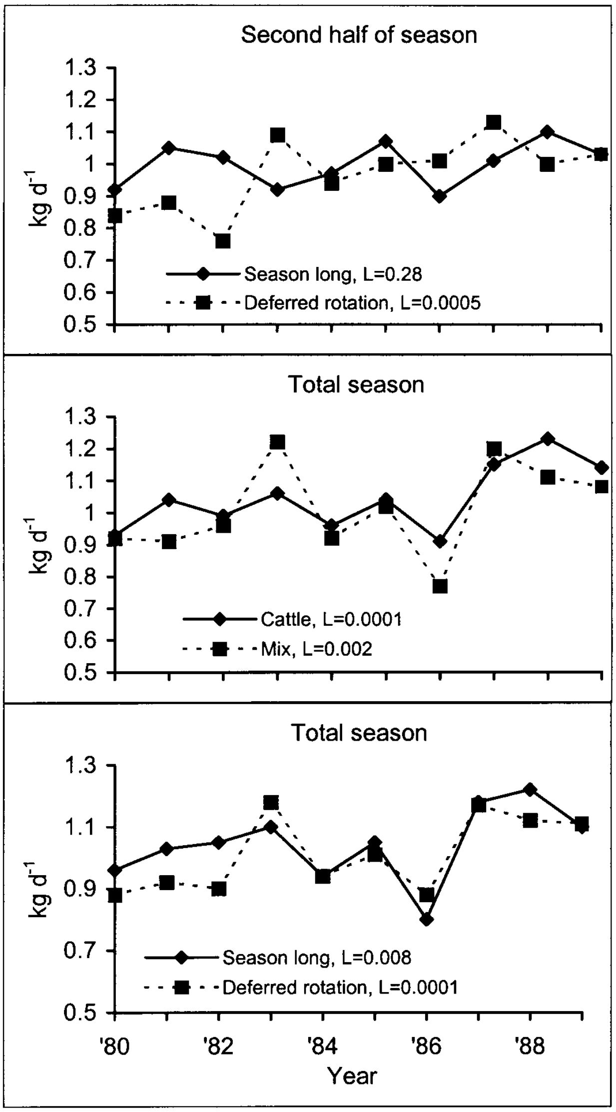

Fig. 2. Mean calf average daily gain (kg day^{-1}) response to significant year X livestock species and year X grazing method interactions. Standard error = 0.11 for years within and across treatments for second half of season responses, and 0.08 for years within treatments and 0.07 for years across treatments for total season responses. In the legends, L refers to the probability of greater F for linear polynomial contrasts.

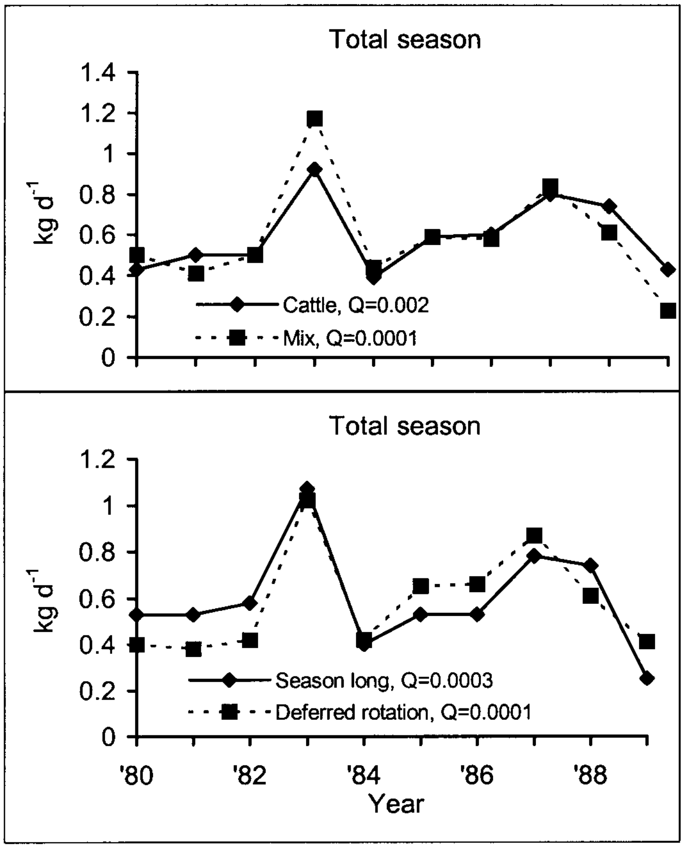

Fig. 3. Mean cow average daily gain (kg day^{-1}) response to significant year X livestock species and year X grazing method interactions. Standard error = 0.11 for years within and across treatments. In the legends, Q refers to the probability of greater F for quadratic polynomial contrasts.

and appear biologically unimportant despite statistical significnace.

Cow ADG varied (P≤0.0003) quadratically across years for all weigh periods (Table 4). Species (P≤0.05) and grazing method (P≤0.02) interacted with year for total season ADG (Fig 3). All treatments displayed quadratic responses in these interactions. Even though trends were similar, interactions occurred because relative ranking of treatment means varied among years. As with calf ADG, these interactions result from small differences that appear biologically unimportant, despite statistical significance. The quadratic responses appear to be similar to the annual precipitation pattern suggesting that nutritional status of mature cows varied with forage conditions, as opposed to the linear increase in ADG over time observed with growing calves. Cow ADG was particularly high in the record-setting wet year of 1983 and particuarly low in 1990, which was the second consecutive year of severe drought.

Lamb average daily gain (ADG) also varied (P=0.0001) among years for all periods (Table 4). First- and second-half ADG changed quadratically (P = 0.0001) across years, but in opposite directions. Thus, total season ADG did not display linear or quadratic responses. Grazing method interacted with year for all periods (P≤0.03, Fig. 4). Both grazing methods displayed the same polynomial contrasts across years as the corresponding year main effects, again indicating that the interaction effect was relatively unimportant. Lamb performance did not show the same linear increase as calf performance.

Ewe ADG varied (P≤0.001) among years for all periods (Table 4). Ewe ADG increased linearly (P=0.003) across years during the first half and responded quadratically (P=0.0001) during the second half and total grazing season. Grazing method interacted with year for first (P=0.0005) and second half (P=0.0001) ADG (Fig. 5). Livestock species also interacted with year (P= 0.04) for second half ADG (Fig. 5). As with lambs, both species and grazing method treatments displayed similar polynomial contrasts across years as the year main effects. Ewe performance also appeared to respond to precipitation conditions, but differences among wet and dry years were not as severe as with cows.

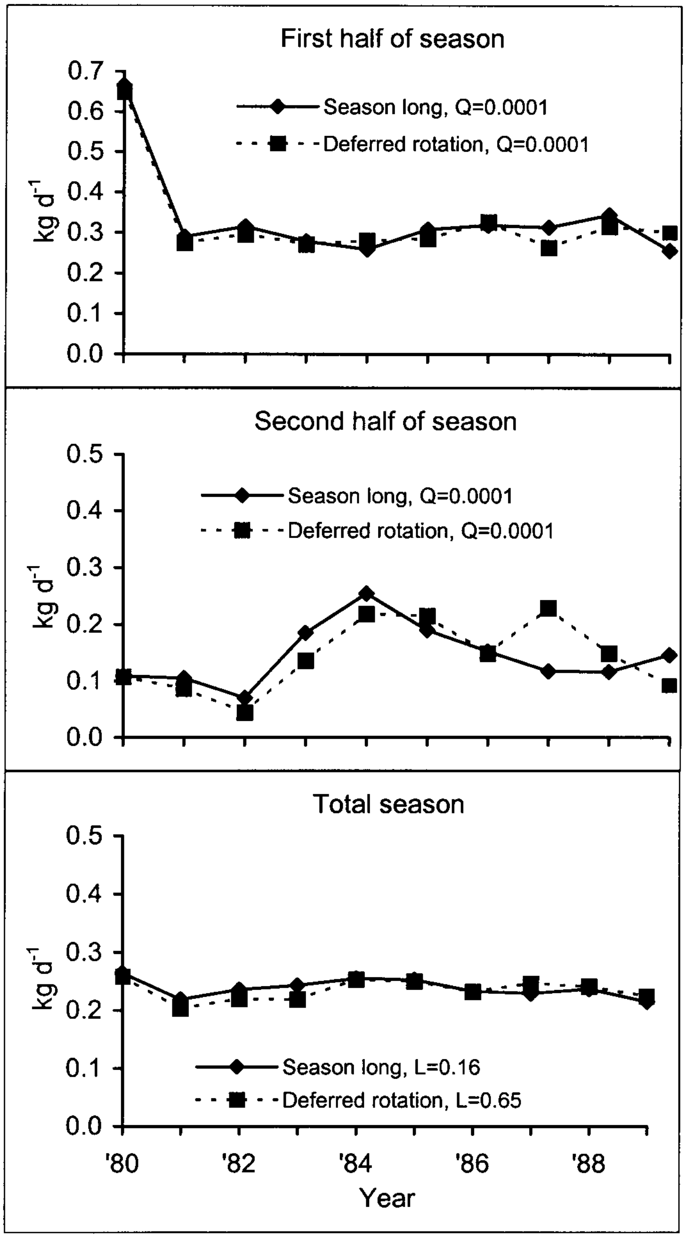

Fig. 4. Mean lamb average daily gain (kg day^{-1}) response to significant year X grazing method interactions. Standard error = 0.016 for years within and across treatments for first half of season responses, 0.021 for years within treatments and 0.020 for years across treatments for second half of season responses, and 0.011 for years within and across treatments for total season responses. In the legends, L and Q refer to the probabilities of greater F for linear and quadratic polynomial contrasts, respectively.

Production per unit land

Mixed species grazing affected gain per ha (Table 5) of progeny (P=0.002), dams (P=0.008), and combined progeny and dams (P=0.009). Production of progeny only and both progeny and dams was similar between mixed species and sheep alone, but less with cattle alone. Production by dams was similar between cattle only and mixed species, but less from ewes alone. Grazing method did not affect (P>0.10) production per ha by any age group (Table 5).

Production per unit of land provides a measure of a system's economic and biological productivity. Increased production by both progeny and dams affects profitability, in that 80% of a given crop of progeny and 20% of dams are marketed annually if a beef or sheep producer practices a typical reproductive female replacement rate of 20%. Because of their larger size, the proportion of gross income from sale of cull dams often exceeds the proportion of the herd culled. Thus, use of mixed species or sheep grazing should promote the greatest economic return to investment in land. In addition, the evaluation of biological productivity per unit land should include both progeny and dams. The 2 livestock species displayed opposite relative rankings in terms of progeny or dam level of production. This appears to be a function of partitioning of nutrient intake by dams into lactation products (progeny growth) vs body energy reserves. Sheep appear to partition a greater portion of nutrition into lamb growth (Matthews et al. 1986). When considering total production by both age groups combined, the greater productivity by cows was masked by progeny production from sheep because the overall level of growth from progeny was much greater than from dams (Tables 2 and 5).

Production per ha varied quadratically among years (P=0.0001) for all 3 age groups (Table 4). Additionally, species interacted with year (P=0.0001) for all 3 age groups (Fig. 6). However, species treatments displayed similar quadratic relationships as corresponding year main effects. This temporal response appeared to follow the precipitation pattern in a similar manner to the majority of animal performance responses.

Conclusions and Implications

Many of the differences among treatments that were statistically significant were so small that they were probably biologically and economically unimportant. However, differences among years, primarily because of weather conditions, were large. For example, production by progeny (kg ha^{-1}) was 60% greater in the best year than the poorest year. This pattern of weather conditions overwhelming treatment responses is common in long-term grazing trials. Keeping the small magnitude of treatment differences in mind, the following conclusions can be drawn about the value of implementing the management practices evaluated herein.

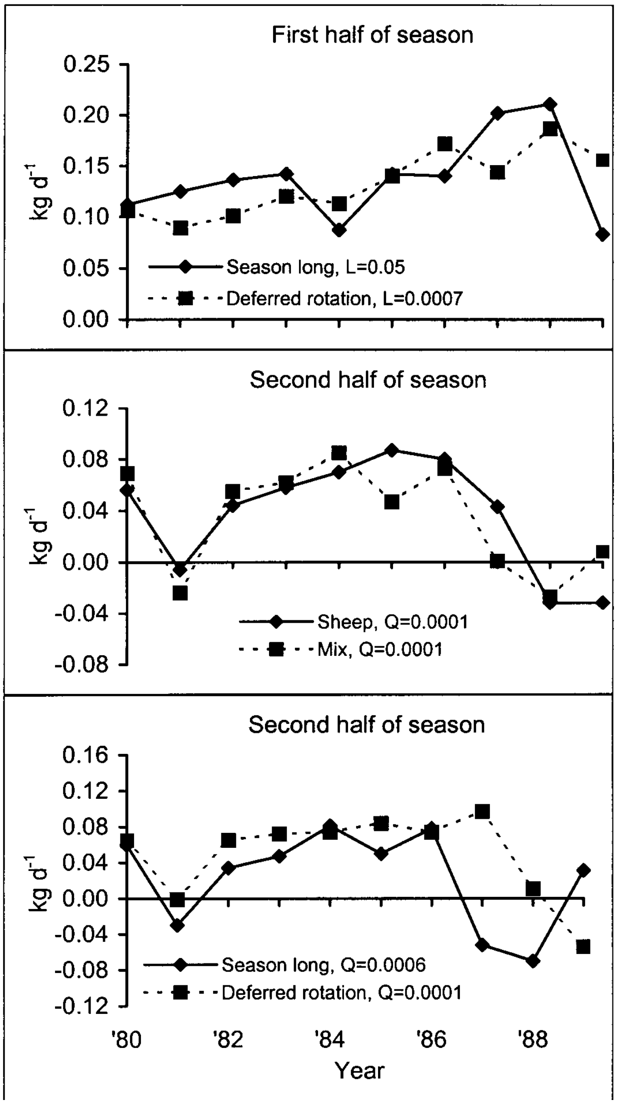

Fig. 5. Mean ewe average daily gain (kg day^{-1}) response to significant year X livestock species and year X grazing method interactions. Standard error = 0.026 for years within treatments and 0.029 for years across treatments for first half of season responses, and 0.024 for years within treatments and 0.023 for years across treatments for second half of season responses. In the legends, L and Q refer to the probabilities of greater F for linear and quadratic polynomial contrasts, respectively.

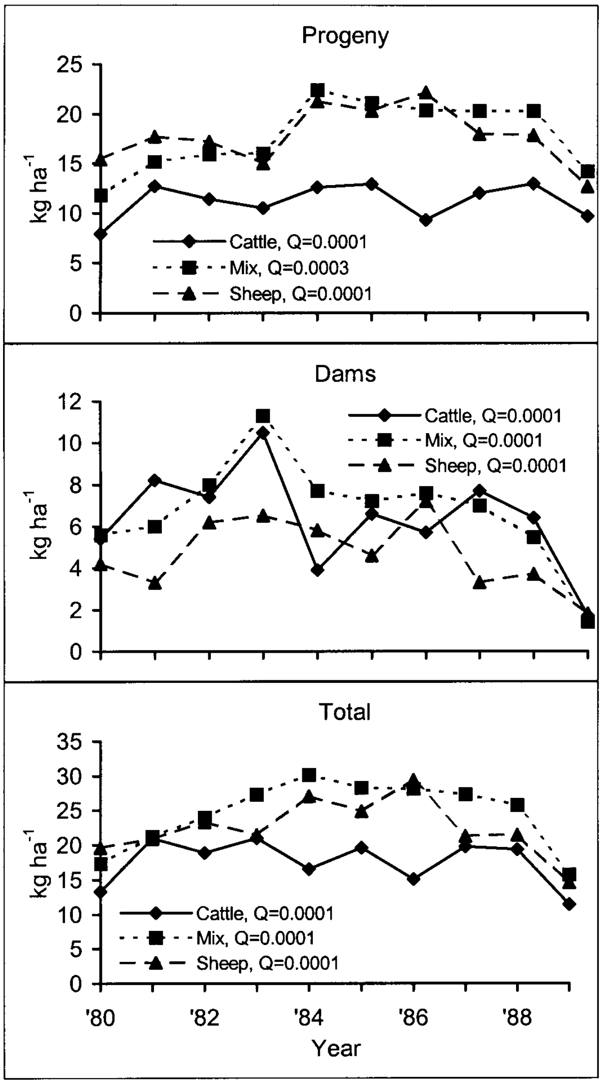

Fig. 6. Mean livestock production (kg ha^{-1}) response by progeny, dams, and total (progeny and dams combined) to year X livestock species interactions. Standard error for progeny = 1.3 for years within species and 1.9 for years across species, 1.2 for years within species and 1.3 for years across species for dams, and 2.1 for years within species and 2.7 for years across species for total. In the legends, Q refers to the probability of greater F for quadratic polynomial contrasts.

Conversion of this rangeland type from historical sheep grazing to mixed species grazing provides a small improvement in rate of weight gain by lambs and ewes. This would yield similar production per unit land of marketable product (progeny), but increased production per ha by dams. Converting from single to mixed species grazing could have other potential benefits, including reduced economic risk by diversification of enterprises and improved cash flow by marketing of multiple products (Walker 1994), reduced loss of sheep to predators because of cow presence, and reduced parasite loads (Baker and Byington 1986). However, total conversion from sheep to cattle does not appear advisable on this vegetation type. While cows and calves performed similarly or slightly better when alone, production per unit land was reduced with cattle only compared to sheep only or mixed species grazing. Additionally, tall larkspur is common in this vegetation type, posing potential toxicity concerns for cattle. However, because sheep are more resistant to larkspur poisoning, their grazing of larkspur under mixed species grazing may decrease cattle poisoning.

Conversion from historical, continuous grazing to deferred-rotation grazing appeared appropriate for a sheep only or mixed species enterprise, primarily because of the improvement in ewe nutritional status shortly before breeding. This appeared to offset reduced calf ADG under deferred-rotation grazing using mixed species. However, if this resource was converted to a cattle enterprise, continuous grazing would be superior because it allowed greater calf performance.

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J. Range Manage.
52:471–480 September 1999

Influence of environmental factors and sheep grazing on an Andean grassland

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Abstract

Chronic overgrazing in the central Andes alters vegetation and may cause erosion and loss of productivity, but quantitative studies are lacking. We measured the relative influence of environmental factors and sheep grazing on local plant species composition, diversity, and soil organic matter in a remote site in northwestern Argentina. Using redundancy analysis, we found that environmental variables explained 22% of variation in species composition between sites, while grazing-related variables explained 24% of variation. The complete model, incorporating all significant variables, explained 33% of variation. Aspect, season of grazing (wet vs. dry) combined with total vegetative cover, and soil type formed the basis for the first 3 ordination axes. Unpalatable or toxic species and very low-growing species were significantly more abundant on heavily grazed sites compared to relatively protected sites. Stocking rate in wet season pastures was negatively correlated with total cover, forage volume, soil organic matter, and species richness. Season of grazing had a more dramatic effect on total cover, forage volume, species diversity and soil organic matter, which were all significantly lower in wet season pastures compared to dry season pastures. Season of grazing and aspect interacted strongly: wet season pastures on north aspects appear more susceptible to degradation and changes in species composition than south-facing sites. Our results suggest that protecting pastures during the summer rainy season may be an important complement to traditional management efforts to reduce stocking rates.

Key Words: Andes, grazing effects, plant ecology, ordination, pastoralism.

Resumen

El sobrepastoreo crónico en los Andes centrales altera la vegetación y puede llegara causar erosión y pérdida de productividad. En el noroeste de Argentina estudiamos la influencia relativa de factores ambientales y pastore por ovejas en la composición y diversidad de plantas, y contenido de materia orgánica en el suelo. Usando una combinación de ordenamientos directos e indirectos, encontramos que las variables ambientales explicaron 22% de la variación en la composición de especies entre sitios,mientras que 24%‘fue explicado por variables relacionadas al pastoreo. Considerando todas las variables significativas se explicó 33% de la variacion Los 3 primeros ejes del ordenamiento estuvieron formados por exposición temporada de pastoreo (húmeda vs seca) junto con cobertura vegetal, y tipo de suelo. Las plantas tóxicas o no palatables, y plantas muy bajas, fueron significativamente más abundantes en sitios con mucha presión de pastoreo. En sitios pastoreados durante la época húmeda, la presión de pastoreo estuvo negativamente correlacionada con la cobertura vegetal total, el volumen de forraje, materia orgánica del suelo y riqueza de especies. La temporada de pastoreo tuvo un efecto más fuerte; los sitios pastoreados durante la temporada húmeda tuvieron menor cobertura total, volumen de forraje, diversidad de especies y materia orgánica en el suelo que los sitios pastoreados en la época seca. La temporada de pastoreo y la exposición interactuaron fuertemente; los sitios pastoreados durante la temporada húmeda en pendientes con exposición Norte parecen más suceptibles a degradarse y a cambiar en composición de especies que los sitios con exposición Sur. Nuestros resultados sugieren que proteger las pasturas durante el verano lluvioso puede ser un complemento importante de los esfuerzos por reducir la carga animal.

Overstocking of Andean rangelands is thought to cause increased erosion (Harden 1993, Molinillo 1993) and loss of productivity (Eckholm 1975, Parker and Alzérreca 1978). Selective grazing, especially by sheep, is usually invoked as the mechanism driving changes in species composition through the replacement of palatable species by coarse bunchgrasses (Ellenburg 1979, Ruthsatz and Fisel 1984). These problems affect virtually all Central Andean highlands

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This research was supported by a 1996-1997 Fulbright fellowship and 1998 N.S.F. Pre-doctoral fellowship to P.B.A. Authors wish to thank Dr. C. Reboratti of the Universidad de Buenos Aires, Ing. R. Neuman and Dr. A.R. Bianchi of INTA , Ing. L. Novara of the Universidad Nacional de Salta, and especially the people of the village of Nazareno for invaluable help and friendship. Special thanks to Ing. A. Sulekik for determining the grass species. Dr. H.R. Grau , Dr. W.K. Lauenroth , Dr. J. Powell, and 3 anonymous reviewers provided helpful comments on early drafts of the manuscript.

Manuscript accepted 11 Nov. 1998.

(Ellenburg 1979, Fjeldsa and Kessler 1996). However, rigorous quantitative studies of the effects of grazing on vegetation and soils are lacking; for example, a review of well over 200 worldwide studies on the effects of grazing on vegetation and soils did not include a single study from the Andes (Milchunas and Lauenroth 1993).

Traditional range management relies heavily on adjustments of the stocking rate to manipulate vegetation condition. Yet the existence of non-reversible changes caused by intense grazing (Biswell 1956, Archer 1989) demonstrates problems with this approach. Current work on non-equilibrium systems suggests that stocking rate may not be the most important determinant of vegetation condition (Ellis and Swift 1988, Westoby et al. 1989). In fact, Turner (1993) found overstocking to be a very poor predictor of degradation potential in an African pastoral system. Especially in arid and semi-arid climates subject to high interannual variation in rainfall, abiotic and stochastic processes may influence ecosystem processes (Biondini and Manske 1996) and vegetation (Wiens 1984, West 1988) far more than biotic interactions such as herbivory.

In light of these findings, management practices should consider the impact of grazing on vegetation relative to other sources of variation. McIntyre and Lavorel (1994) provided a model for studying how an exogenous disturbance overlays patterns of vegetation related to the physiographic environment. Working in a semi-arid Australian rangeland, they used canonical correspondence analysis to quantify the amount of variation in species composition explained by environmental versus disturbance variables. They also identified significant associations between individual plant species and various environmental and grazing-related factors.

McIntyre and Lavorel's (1994) approach allows us to describe the vegetation of a poorly studied grassland community in the Andes of northwestern Argentina while simultaneously quantifying the local impact of intense sheep grazing. Specifically, we aim to 1) determine the relative influence of grazing and environmental variables on plant species composition, and 2) show the effect of grazing on individual plant species and on stand-level variables such as total cover, species richness, and soil organic matter.

Methods

Study Area

The Cordillera Oriental of northwestern Argentina is remote and undeveloped, an extremely rugged area (Fig. 1) where subsistence remains the most important economic activity (Reboratti 1996). Few studies have examined the transitional grasslands between cloud forests and high desert, the focus of human activity in the region. Viera and Menéndez (1981) mapped geomorphic features and vegetation from aerial photos and Mendiola (1996) described plant species composition.

The study area surrounds the village of Nazareno in Salta province (22°30'S, 65°70'W) located at an elevation of 3,000 m. (Fig. 2). The site is influenced

Fig. 1. The valley of the Río Nazareno and the village of Cuesta Azul, at the southern end of the study area.

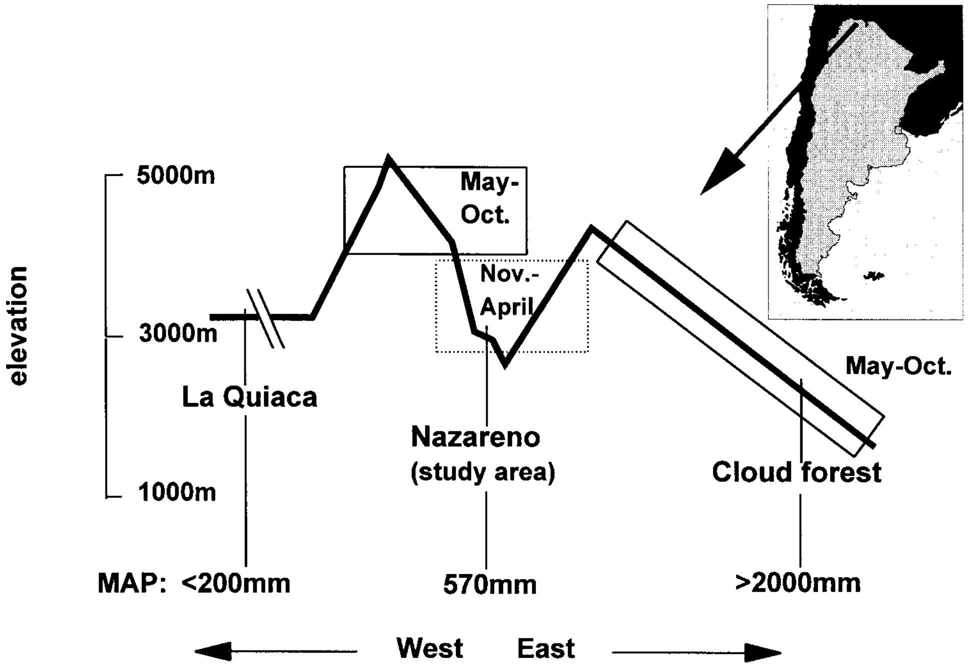

Fig. 2. Location of study site in northern Salta province, Argentina, and schematic elevation profile showing annual precipitation and pastoral movements.

by strong elevation and precipitation gradients. From October through April, the austral summer, air traveling westward from the Atlantic rises up the east slope of the Andes, drops most of its moisture over the rain and cloud forests, then becomes progressively drier. Mean annual rainfall declines from 2,000 mm at 1,000 m elevation at the eastern edge of the Andes to less than 200 mm in La Quiaca , on the Puna , or Altiplano (Bianchi 1981). Nazareno, in between these 2 extremes, receives 574 mm/yr^{-1} (pers. comm. EVARSA, a regional utility). Seasonality is extreme, with virtually all rainfall occurring between October and April. Inter-annual variation in rainfall is low; in the 7 years of data available for Nazareno, annual rainfall ranged from 490 mm to 640 mm. Total precipitation during the study year was 597 mm, slightly above the mean. Frosts are frequent from April to October (Bianchi 1981). Steep slopes and weak sedimentary rock make the area highly susceptible to erosion and mass movement (Viera and Menendez 1981). Soils are shallow, rocky lithosoles with little organic material (Nadir 1990). The texture is sandy-loam with a high percentage of gravel, although within the study area deep pockets of clay-loam are frequent as well. Vegetation is characterized by large perennial bunch grasses (especially *Stipa* and *Festuca* species), interspersed with scattered shrubs such as *Baccharis, Adesmia,* and *Senna* species.

Pastoral System and Stocking Rates

Most pastoralists near Nazareno follow a transhumant strategy in response to seasonal fluctuations of forage availability. Women or children move the family's herd of typically 50 to 150 sheep and goats to the high mountains following the harvest, then to the montane forests during the winter dry season, before returning to their villages for the summer wet season (Fig. 2). The variety of movements makes generalization difficult, and some families graze their sheep and goats year-round near their permanent home in the valley. This study focuses solely on the valley pastures surrounding Nazareno and its neighboring villages.

Almost all rangelands in the valley are communal in a legal sense, but each family retains rights through long-standing tradition to a particular sector usually surrounding their home. These zones of roughly 50 ha (with great variation) may overlap, but their boundaries are recognized and respected. Scattered within this heavily grazed matrix are small areas of natural vegetation contained within fences built to protect agricultural fields from livestock, or to maintain dry season forage reserves. Not grazed until after the harvest in May, these protected sites are exceptions to the widespread wet season grazing in the valley and were sampled as "dry season" sites. They range in size from 1 ha to approximately 20 ha and are composed of the same vegetation as the adjacent "wet season" pastures.

Sheep are the dominant form of livestock, though horses, burros, and cattle are common. Our estimations of stocking rates include only sheep grazing for the following reasons: first, because horses graze very close to the houses, and cattle generally high in the mountains or near the cloud forests, sheep are the principal grazers on most of the valley rangelands. Second, since sheep are taken to pasture every day by a shepherd and are confined to the family's sector, their movements can be easily mapped, in contrast to the free-ranging cattle. Based on conversations with the pastoralists, most families have maintained a fairly constant herd size for at least a generation. Our study therefore concerns the effects of historical, rather than single-year, sheep grazing.

To calculate stocking rates during the wet season, we collaborated with workers from a livestock production program initiated by the Spanish missionary organization OCLADE (Obras Claretianas para el Desarollo). These extension workers showed us each pastoralist's grazing sector and supplied census information on the size and composition of their herd, and the length of time the animals remain in the sector each year. This information was supplemented by informal interviews with the pastoralists. Using aerial photos to estimate the surface area of each sector, we calculated the number of sheep and goat days per hectare. Before further statistical analysis, we divided the stocking rate (sheep and goat-days ha^{-1}) by a logarithm of the distance between the corral and the sampling site, assuming grazing intensity within each sector decreases with distance from the corral.

We were unable to calculate stocking rate for the dry season sites. Grazing on these small pastures is generally concentrated in an intense pulse during the 3 or 4 weeks following harvest and all species—horses, burros and cattle, in addition to sheep and goats—are present. Therefore, our analysis of the effect of stocking rate is limited to the subset of sites grazed during the wet season, while that of the effect of season of grazing includes all sites.

Vegetation Sampling

We sampled in upland natural grasslands extending 10 km north and 8 km south from the village of Nazareno, on the west side of the Río Nazareno. We attempted to minimize site-to-site variation in altitude, which would otherwise be the dominant influence on vegetation in this high-relief landscape (sampled sites ranged from 2,914 to 3,383 meters above sea level). Sites fall into 2 broad land-use categories: pastures grazed during the summer wet season and pastures grazed only during the winter dry season. Between January and March of 1997, fifty-seven plant surveys were completed along a trail contouring at a relatively even elevation on small east-west trending ridges. In general, we sampled 1 site on both the north and the south aspect of each ridge, locating the site subjectively in a patch of the most representative vegetation. Forty sites were located in summer wet season pastures; 17 sites were located in winter dry season pastures. At the time of sampling, dry season pastures had not yet been grazed.

We measured species composition and cover using 2 paired 10-meter line intercept transects, recording the cover of all plant species, rock, and bare ground. The parallel transects, 10 meters apart, ran with the slope, to cross the ubiquitous stock trails at a 90° degree angle. Botanical nomenclature follows Cabrera (1977–1983). We also estimated the average height of all plant species on each transect. Environmental variables including aspect (2 classes: north and south), slope, and elevation were measured. A sample of the first 10 cm of soil was collected from between the transects. Soil samples were analyzed for organic carbon and total organic material at the Instituto Nacional de Tecnología, Agropecuaria (INTA) in Cerrillos, Salta, using a wet combustion method (Walkley and Black 1934). Before samples were prepared for analysis, technicians classed soil texture qualitatively.

Information on palatability of plant species was gathered from pastoralists and Fernandez et al. (1992). "High" palatability indicates species always consumed. "Medium"describes plants which may be palatable at only 1 time of the year (usually at the start of the growing season) or eaten only in the absence of more palatable alternatives. "Poor" palatability is reserved for species that are minimally consumed and toxic species. The large number of species for which we had no information were excluded from this analysis. Using plant height and cover we calculated biovolume, a proxy for biomass (dePietri 1992). The biovolume of palatable species was summed to yield "forage volume."

Data Analysis

Ordination techniques can be used to characterize community level responses to environmental and disturbance variables, as well as to identify species sensitive to particular factors. Ordination axes can be constrained as linear combinations of a priori defined or measured variables associated with species records. As in general linear models, these variables can be combined in a stepwise manner (ter Braak and Prentice 1988). To further test independence, ordinations can be conducted after the effects of a variable or set of variables has been removed (partial analysis, Borcard et al. 1992, Okland and Eilertsen 1994).

To decide whether to use eigenvector techniques based on unimodal or linear species responses, we made scatter plots of species abundance and some of the environmental gradients, and considered the "length of gradient" measured in standard deviation units obtained by detrended correspondence analysis (DCA). After judging by eye that most species showed nearly linear responses within the observed range, and having obtained relatively short gradients in DCA ordinations (always less than 3 SD), we decided to use redundancy analysis (RDA) as our constrained ordination technique.

In the CANOCO version of RDA the fraction of the total variation in the species matrix "explained' by a variable or set of variables can be directly read from the sums of constrained eigenvalues (Jongman et al. 1987, Borcard et al 1992). We used 99 unrestricted permutations of the constraining variable (Monte Carlo test in CANOCO, ter Braak 1990a) to assess the statistical significance of each variable. The terms "explanation" and "variation explained" are used here in a statistical sense rather than implying cause and effect. As infrequent species of random occurrence can give rise to spurious effects (Jongman et al. 1987), we excluded from the analysis species with frequency lower than 5% (66 taxa excluded, 115 included). All cover data were log-transformed to prevent high-cover species from disproportionately influencing the analysis.

To study the effects of environment and grazing we followed McIntyre and Lavorel (1994). First, we looked for significant structuring of the species data in relation to environmental variables and their interactions (aspect: north or south; soil type: clay-loam or sandy-loam; slope; elevation). Second, we quantified the effects of the grazing-related factors (stocking rate in wet season pastures; season of grazing: wet or dry; total vegetative cover; soil organic matter; date of sampling). "Grazing-related factors" are either management practices, variables directly affected by grazing, or, in the case of date of sampling, a rapidly changing variable in comparison to the "fixed" environmental factors. Third, we put both environmental and grazing factors into 1 complete model and used partial ordination to study the effects of grazing regime once environmental effects had been taken into account. In each model, variables were included in forward stepwise selection after satisfying a Monte Carlo test.

Since Redundancy Analysis (RDA) is a form of multivariate multiple regression the results of the analysis include regression coefficients and associated t-values. An objective way to identify individual species significantly correlated with explanatory variables in RDA is by examining the t-value biplots, which are 2-dimensional graphs showing the t-values of the regression coefficients for a given species on the explanatory variables (ter Braak 1990b). We used this technique to classify species according to their association with environmental and grazing related factors. All analysis were performed using the program CANOCO version 3.12 (ter Braak 1987, 1990a).

To evaluate the effect of stocking rate (wet season pastures only) on stand-level variables, we performed a rank transformation of stocking rate, then used Spearman rank order correlations. To test differences in these variables caused by season of grazing and aspect, one-way ANOVA was used. We tested the relationship between grazing response and species palatability and stature with a non-parametric ANOVA (Kruskal-Wallis H) using species' scores from the ordination. For these tests we used SPSS 8.0 for Windows and rejected the null hypothesis at *P* <05.

Table 1. Test of significance of explanatory variables for species composition. "Variation Explained" = eigenvalue of constrained axis divided by the sum of all eigenvalues. Variables included in the complete model are shown in boldface, with percent variation explained once incorporated in the model in brackets. P=significance probability of the constrained axis in a Monte Carlo permutation test (H_0=influence of variable not significantly different from random).

Variables	Variation Explained	P
a. Environmental variables	(%)	
Elevation	2.0	0.66
Aspect	**10.2** (8.0)	0.01
Soil	**6.4** (6.1)	0.01
Slope	4.3	0.01
Elevation*Aspect	11.2	0.10
Elevation*Soil	8.5	0.07
Elevation*Slope	2.5	0.04
Aspect*Soil	18.8	0.01
Aspect*Slope	13.3	0.01
Soil*Slope	10.7	0.01
Aspect*Soil+Slope	21.6	0.01
b. Grazing-related variables		
Date (day of sampling)	**4.6** (2.5)	0.02
Season (of grazing)	**9.4** (4.5)	0.01
Stocking rate (sheep-days/Ha)	7.8	0.01
Total cover	**10.2** (4.7)	0.01
Soil organic matter	7.1	0.01
Cover+Season+S.O.M.+Date	23.6	0.01

Table 2. Eigenvalues of the first 4 axes in the complete model RDA and correlation coefficients with the environmental and grazing variables. Total=sum of all eigenvalues. Boldface indicates the factor most strongly correlated with each axis.

	Axis 1	Axis 2	Axis 3	Axix 4	Total
Eigenvalue	0.1142	0.1032	0.0571	0.0388	0.332
Aspect	**–0.8292**	0.3649	0.3792	0.1628	
Soil Type	–0.3566	–0.0117	**–0.9242**	0.1019	
Date (of sampling)	0.0825	0.5490	0.0488	–0.2210	
Season of Grazing	–0.2312	**–0.9006**	0.0564	0.2454	
Total Cover	0.6347	0.7126	–0.0053	0.2856	

Results and Discussion

Effects of Environmental Variables on Species Composition

Each environmental factor except altitude, which we limited to a range of less than 400 m, explained a small but significant proportion of variation in species performance (Table 1a). Aspect accounted for the highest inter-site variability in species composition (see Appendix for species list). A total of 19 species were recorded exclusively in sites facing south but only 4 species were found exclusively in sites facing north. Soil type was ranked second in amount of variation explained. Eight species were found exclusively at sandy-loam sites and 4 species were recorded only at clay-loam sites.

The combination of aspect and soil type explained 19% of total variation. In this ordination, the first axis separates north and south aspects, while the second axis separates sandy-loam from clay-loam soils. After incorporating the combined effects of aspect and soil type, the only environmental variable that could significantly increase the amount of variation explained was slope. The "best fitting" model based on environmental variables accounted for 22 % of total variation (Table 1a).

Effects of Grazing-related Factors

Differences in total vegetation cover and season of grazing were the most important factors accounting for variation in species composition. Stocking rate and season of grazing had similar explanatory power when taken independently (Table 1b). However, once the effects of season of grazing were incorporated into the model, stocking rate was no longer significant. The model incorporating all significant variables (cover, season, organic matter, and date of sampling) explained 24% of the total inter-site variability in species composition. This value is slightly higher than the best fitting environmental model.

In this ordination of grazing-related factors, the first axis related to the contrast between total cover and season. High cover sites correlate with sites protected during the wet season, low cover sites correlate with sites grazed during the wet season. The second axis was associated with organic matter content, and the fourth axis was dominated by date of sampling. The first 2 axes accounted for 79% of the total (24%) variation explained by the set of grazing related variables.

The importance of grazing relative to environmental factors attests to the intensity of land-use in this landscape. In fact, we may have underestimated the influence of land-use due to a lack of information on 2 potentially important sources of variation, historical grazing patterns and the traditional use of fire to stimulate early season growth.

Combined Effects of Environmental and Grazing Factors

The complete model, which incorporates in a stepwise manner both environmental and grazing related variables, accounted for 33% of the total variation in the species matrix (Table 2), similar to comparable studies (Lavorel et al. 1991, McIntyre and Lavorel 1994). In this ordination the first axis is related to aspect, the second axis captures variation related to season of grazing and

Table 3. Individual species affected significantly (t-value biplot score |<|1|) by season of grazing in the complete model RDA.

Family	Species	T-value Biplot	Variation Explained	Palatability
a. Wet Season Pasture Species			%	
Apiaceae	*Bowlesia* cf. *pulchella* Wedd	–0.476	23.09	unknown
Asteraceae	*Baccharis multiflosculosa* Heering	–0.484	17.07	poor
Poaceae	*Stipa ichu* (R. et P.) Kunth	–0.625	14.28	poor
Poaceae	*Nasella pampagrandensis* (Spreg.) Barkworth	–0.695	10.21	poor
Oxalidaceae	Oxalis argentina Knuth	–0.702	9.78	medium
Asteracea	*Achyrocline ramosissima* Sch. Bip.	–0.740	10.04	unknown
Pteridophyta spp.		–0.885	7.72	poor
Convolvulaceae	*Dichondra sericea* v. *microcalyx* Sw.	–0.887	6.76	medium
Poaceae	*Sporobolus indicus* (L.) R. Br.	–0.904	8.21	poor
Poaceae	*Bromus catharticus* Vahl.	–0.907	5.26	high
Fabaceae	*Senna alata* (L.)Rox.	–0.909	7.94	medium
b. Protected Site Species				
Asteraceae	*Tagetes minuta* Linn.	0.462	18.65	medium
Poaceae	*Diplachne dubia* (HBK) Scribn.	0.598	17.18	high
Asteraceae	*Stevia minor* Gris.	0.624	11.84	medium
Poaceae	*Lycurus phalaroides* Kuntze	0.628	15.55	unknown
Poaceae	*Paspalum humboldtianum* Flugge	0.695	13.78	high
Oxalidaceae	*Hypseocharis tridentata* Griseb.	0.730	10.39	high
Asteraceae	*Gutierrezia mandonii* Sch. Bip.	0.786	9.19	medium
Asteraceae	*Hypochoeris elata* Wedd.	0.854	5.37	medium
Poaceae	*Botriochloa* sp.	0.897	7.71	medium
Convolvulaceae	*Ipomoea minuta* f. *minuta* R. Fries	0.925	7.92	poor
Poaceae	*Muhlenbergia rigida* (HBK) Trino	0.944	5.07	medium
Poaceae	*Deyeuxia tarmensis* Pilg.	0.977	4.54	medium
Poaceae	*Festuca* spp.	0.984	4.76	medium

total cover, while the third axis represents variation due to soil type. Except for covariation of total cover with both aspect and season, the primary 3 factors (aspect, season, and soil type) are largely orthogonal (Table 2).

Partial ordination of grazing related factors once the environmental factors were taken into account explained 16% of the species matrix. This implies that one-third (8% out of 24%) of variation explained by grazing related factors was structured in the environmental matrix. Again, total cover and season were the most important variables.

Effects on Individual Species

T-value biplots indicated that species were significantly associated with grazing (Table 3) and environmental factors (see Appendix). Perennial grasses were particularly sensitive to wet versus dry season grazing. *Stipa ichu* (R. et P.) Kunth and *Nasella pampagrandensis* (Spreg.) Barkworth were indicators for sites grazed in the wet season, while *Diplachne dubia* (HBK) Scribn., *Lycurus phalaroides* Kuntze, *Paspalum humboldtianum* Flugge and *Festuca* spp. were characteristic of dry season pastures. If associations with total cover are also considered, the highly palatable *Trifolium amabile* Kunth, a very common species, should be added to the list of indicators for dry season or lightly grazed sites.

In a non-parametric 1-way analysis-of-variance, individual species scores on the grazing-related axis 2 of the complete ordination were significantly related to palatability (Table 4). The rank means for the medium and high palatability classes were similar, while the rank mean for the poor palatability class was much lower. Low-growing species were significantly more common on the heavily-grazed sites (Table 4). This effect was strongest when species less than 7 cm were compared to all taller species, and became insignificant when the limit of the short class was moved up to 15 cm.

These results support the prevailing view in the Andes that changes in species composition due to grazing are driven by differential palatability. As previous research has indicated, *Stipa ichu*, a typical coarse, unpalatable bunchgrass, is characteristic of heavily-grazed wet season pastures (Ellenburg 1979, Ruthsatz and Fisel 1984). Avoidance of highly unpalatable and toxic species appears to be more important than selection of highly palatable species, which were treated no differently than species of medium palatability.

The shift in composition to plants of lower stature on heavily-grazed sites suggests other possible mechanisms for differential response to grazing. Plants able to grow very low to the ground either avoid grazing, or have superior physiological responses to grazing compared to taller plants. Other studies in the Andes (Wilcox et al. 1987) and elsewhere (Noy -Meir et al. 1989, Belsky 1992) have identified the same pattern.

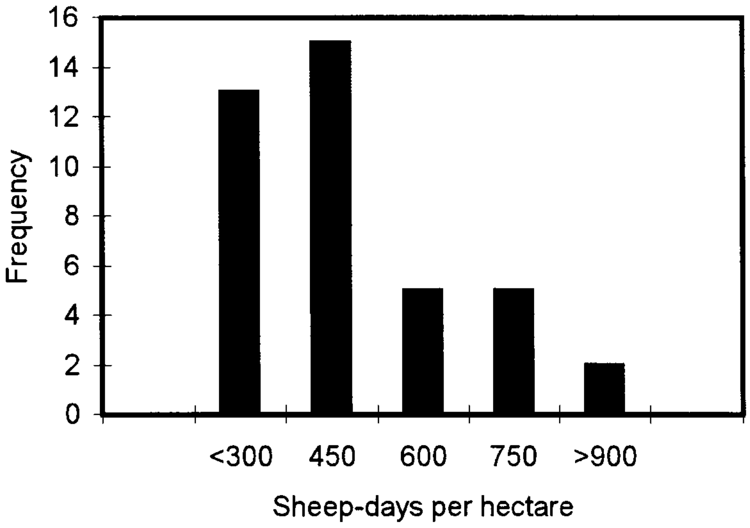

Fig. 3. Frequency distribution of stocking rates among the 40 wet season pastures.

Table 4. Palatability and plant stature affect species' scores on the grazing related axis II of the complete ordination in non-parametric one-way ANOVA (Kruskal-Wallis H.) The effect of plant stature weakens as the limit between the short and tall class is increased.

Variable and Class	N	Mean Rank	χ^2	P
Palatability			*df*=2	
Poor	21	28.6	6.22	.05
Medium	38	40.9		
High	17	45.3		
Plant stature			*df*=1	
<7 cm	41	46.2	7.92	.01
>7 cm	74	64.5		
<15 cm	72	54.1	2.62	.11
>15 cm	43	64.5		

Table 5. Spearman Rank Order Correlations among variables in wet season pasture site (n=40).

Variables	Spearman R	t (n-2)	P
Stocking rate & Total cover	–0.54	–3.95	.01
Stocking rate & Richness	–0.36	–2.41	.02
Stocking rate & Soil organic matter	–0.37	–2.41	.02
Stocking rate & Forage volume	–0.25	–1.62	.11
Total cover & Richness	0.61	4.69	.01
Total cover & Soil organic matter	0.58	4.42	.01
Total cover & Forage volume	0.58	4.41	.01

Table 6. Differences between dry season (n=17) and wet season (n=40) pastures, using one-way ANOVA.

Response Variable	Mean Dry Season Sites	Mean Wet Season Sites	F	P
Total cover (%)	133.0	67.0	51.42	.01
Forage (cm^3)	1501.0	208.0	42.01	.01
H (Shannon-Weiner)	3.9	3.5	7.46	.01
Soil organic matter (%)	4.3	3.1	4.18	.05
Richness	39.5	35.9	2.33	.13

Table 7. Mean percent cover and standard error of the mean (in parantheses) of important vegetation classes grouped by site aspect and season of grazing. Sample sizes are as follows: wet season*N=20, wet season*S=20, dry season*N=9, dry season*S=8.

Aspect	Cover class	Wet season	Dry season
		(%)	
N	Grasses	27.1 (4.5)	62.3(5.8)
	Forbs	16.4 (2.6)	49.9 (6.7)
	Shrubs	8.7 (2.4)	15.6 (4.8)
	Ferns	1.4 (0.4)	0.5 (0.2)
	Bare ground	43.2 (4.3)	6.2 (3.2)
S	Grasses	40.1 (3.1)	65.2 (6.7)
	Forbs	20.2 (2.1)	39.7 (5.7)
	Shrubs	19.6 (5.5)	31.7 (6.1)
	Ferns	1.5 (0.4)	0.2 (0.1)
	Bare ground	18.4 (2.7)	3.0 (1.2)

We could not confirm the significance of plant growth form (dePietri 1992) in determining species-level response, nor do we have data on species' physiological response. Fine-scale spatial relationships may be important as well: palatable species seemed to "hide" under larger shrubs.

Stand-level Variables

The mean stocking rate in wet season pastures was 362 sheep and goat-days ha^{-1} each 6 month wet season, and ranged from 154 to 793 (Figure 3). The Spearman rank order correlations show significant inverse relationships between stocking rate in wet-season pastures and total cover, species richness, soil organic matter and forage volume (Table 5). Total cover is positively correlated with richness, soil organic matter, and forage volume (Table 5). Total cover may be as effective as stocking rate as an indicator of site condition.

Differences between wet season and dry season pastures are dramatic. Dry season pastures have much higher total cover, forage volume, plant species diversity, and soil organic matter (Table 6). Season of grazing did not significantly affect richness.

Aspect had a strong effect on stand-level variables, consistent with its influence on species composition. Forage volume, total cover, species richness and soil organic matter were much higher in wet season pastures on south aspects compared to north aspects (one-way ANOVA, n=40, all F's >8.00, all P <.01). In dry season pastures, only soil organic matter was significantly higher on south aspects (n=16, F=6.06, P =.026). This apparent interaction between aspect and season of grazing (Table 7) led us to revisit our analysis of species composition. In the complete model Redundancy Analysis (RDA), an aspect*season of grazing interaction explained over 3% of variation in species composition even when aspect and season were included as covariables

Such a marked contrast between north and south slopes may not only be due to differences in solar radiation, but also to condensation from low clouds carried by the prevailing southerly winds in the summer wet season. These páramo-type grasslands have been termed "cloud pastures," analogous to cloud forests (Brown and Grau 1993), and unmeasured precipitation may be considerable, especially on southern aspects. South facing slopes, which probably receive and retain more water than north slopes, are apparently more resistant to degradation caused by wet season grazing.

The Importance of Season of Grazing Compared to Stocking Rate

Whether or not a site is grazed during the summer wet season, when vegetation is active, emerged as a critical determinant of both species composition and stand-level variables. Because we have no data on stocking rates during the dry season, it is possible that dry season grazing intensities are much lower than in the wet season, meaning that difference between wet and dry season pastures would be essentially a difference in stocking rate. Given the very small size of the dry season pastures and the intensity of land-use in the area, this seems unlikely. The shorter length of rotation could also explain the lesser impact of dry season grazing. However, previous work has shown that the effects of sheep grazing on vegetation do in fact depend on the season of grazing (Bork et al. 1998). The importance of protecting vegetation during the season of active growth and reproduction has been reported in other grazing systems as well (Bartolome 1993, Brown and Stuth 1993).

We can suggest a number of mechanisms for the severe impact of wet season grazing. Many species are only palatable during the early growing season and would be avoided in the dry season (Molinillo and Monasterio 1997), making it likely that less biomass is removed during dry season grazing. Trampling is more damaging when plants are active and soil wet and soft (Heady and Child 1994). Resulting soil compaction can dramatically alter hydrology, lowering infiltration and raising sediment production (Warren et al. 1986). Grazing during the reproductive season also can cause seed loss (Bertiller 1994). Finally, soil nutrient status, which may influence species composition (Tilman 1990), would be affected by both biomass removal and increased erosive action.

Stocking rate in the wet season was less effective than both season of grazing and total cover in explaining variation in species composition and differences in stand-level variables. Clearly, the difficulties of measuring stocking rate in this complex, fenceless landscape hamper prediction. Without better estimations of stocking rate during both wet and dry seasons, we cannot exclude stocking rate as an important factor. However, it is possible that as Turner (1993) found in Africa, stocking rate may simply be a poor indicator of degradation potential.

Management Implications

Proposed management solutions in the Andes have generally focused on the need to reduce the total number of stock (LeBaron et al. 1979). Our findings suggest that protecting grasslands during the rainy season should at least complement if not significantly improve upon strategies based on reductions in stock. For example, we might suggest that the traditional annual rotation of herds through the landscape (from valley to cloud forest to high peaks) could be altered between years, allowing the valley pastures to rest in one rainy season, and the high peak pastures to rest in another. A second alternative to provide wet season protection would require further concentrating grazing pressure in some areas in order to rest others. If already degraded pastures prove stable under increased use, a reasonable possibility given the area's history of degradation, and if rested pastures do indeed recover, then the benefit of protecting one pasture might outweigh the cost of concentrating grazing on another pasture.

However, we present these alternatives pessimistically. The subsistence requirements of poor rural communities in the Central Andes, combined with environmental and cultural constraints, severely limit the potential for any management change (Browman 1987). Altering transhumant patterns, as we suggest in our first alternative, would force shepherds and their flocks to endure harsh, wet conditions among the peaks while missing Christmas and Carnaval in the valley villages, the most important social reunions of the year. Protecting areas within the wet season pastures, as in our second alternative, may be impossible without fences or the capital to construct them. On the other hand, the dramatic cultural and economic transformations affecting this region, initiated by greater integration with the national and global economy (Reboratti 1996), may generate novel perspectives and foster new approaches.

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See appendix on page 480 and 481.

Appendix. Frequency of occurrence, F(%), of plant taxa recorded in 57 sites in Nazareno, Depto. Santa Victoria, Salta, Argentina, from January through March, 1997. Species with a frequency less than 7% were not included in the ordination and are not listed. Associations of taxa with environmental and grazing factors as indicated by RDA are as follows: Aspect: N=North, S=South; Soil type: Cly=Clay-loam, Sdy=Sandy-loam, Phenology: -Phe=early, +Phe=late; Grazing regime: Wet=wet season pasture, Dry=Dry season pasture; Total cover: +Cov=high cover, -Cov=low cover.

F (%)	Species	class
86.0	*Bidens pseudocosmos /B.exigua* Sherff	N, +Cov
86.0	*Trifolium amabile* Kunth	+Cov
78.9	*Dichondra sericea v. . microcalyx* Sw	N, Cly, Wet, +Cov
78.9	*Plantago tomentosa* Lam.	S
78.9	*Stipa ichu* (R. et P.) Kunth	Wet, +Cov
71.9	*Tagetes pusilla* Humb.	N, Sdy
66.7	*Eragrostis andicola* Fries	N, Sdy
66.7	*Rebulnium richardianum* Gillies	S
64.9	*Microchloa indica* (Lif.) P. Beauv.	
63.2	*Oxalis argentina* Knuth	S, Wet
57.9	*Muhlenbergia rigida* (HBK) Trino	N, Sdy
52.6	*Hypochoeris elata* Wedd.	S, Dry
49.1	*Bromus catharticus* Vahl.	S, -Phe, Wet, +Cov
49.1	*Stevia minor* Gris.	Dry
47.4	*Elyonurus muticus*(Spreng.) Kuntze	Sdy
45.6	*Nasella pampagrandensis* (Spreg.) Barkworth	S, Wet, +Cov
45.6	*Poa* sp.	S
43.9	*Ipomoea minuta f.minuta* R. Fries	Dry
42.1	*Cheilanthes pruinata* Kaulf.	Sdy
42.1	*Cyperus andinus* Palla ex Kuk	S
42.1	*Richardia stellaris* Cham.	N, Sdy
40.4	*Allium* spp.	S
40.4	*Hypochoeris meyeniana* v. *meyeniana* Walp	Cly, +Phe, -Cov
38.6	*Bidens mandonii* Sherff	N
38.6	*Festuca* spp.	S
36.8	*Arenaria lanuginosa* (Michaux) Rohrb.	
36.8	*Belloa punae* Cabr.	S, +Phe
36.8	*Pteridophyta* spp.	Sdy, Wet, +Cov
35.1	*Galinsoga unixioides* Gris.	+Cov
33.3	*Aristida adscensionis* v. *modesta* Hack.	N, Sdy
33.3	*Deyeuxia tarmensis* Pilg.	S
33.3	*Euphorbia prostrata* Aiton.	
33.3	*Stipa pseudoichu* Caro	N, -Phe, +Cov
31.6	*Vulpia myuros* (L.) Gmel. forma *megalura* (Nutt.) Stace & Cotton	N
29.8	*Baccharis multiflosculosa* Heering	-Phe, Wet, +Cov
29.8	*Nasella mucronata* (HBK) Pehl	
29.8	*Stenandrium dulc*e Car.	
28.1	*Bowlesia* aff. *pulchella* Wedd.	Wet, +Cov
26.3	*Astragalus garbancillo* Cav.	N, Cly
26.3	*Cynodon hirsutus* Stent.	
26.3	*Gamochaeta subfalcata* Cabr.	
26.3	*Iridaceae* sp.	
24.6	*Adesmia* aff. *cytisoides* "A" Griseb.	S, +Phe
24.6	*Chondrosum simplex* (Lag.) Kunth	N, +Phe
24.6	*Crassulaceae* sp.	
24.6	*Erodium cicutarium* (L.) L'Hér. ex Aiton	
24.6	*Hypseocharis tridentata* Griseb.	N, Dry
24.6	*Pennisetum chilense* (Desv.) B.D. Jackdon ex R.E. Fr.	+Cov
24.6	*Satureja parviflora* (Phil.) Epling	S
24.6	*Tagetes minuta* Linn.	Dry
22.8	*Parthenium hysteriophorous* L.	N, Cly
21.1	*Achyrocline ramosissima* Sch. Bip.	Sdy, Wet, +Cov
21.1	*Lepechinia meyenii* Walp.	Sdy
21.1	*Lycurus phalaroides* Kuntze	Dry
21.1	*Sisyrinchium chilense* Hook.	
21.1	*Viguiera tucumanensis* Hook.	
21.1	*Zinnia peruviana* (L.) L.	
19.3	*Adesmia aff. cytisoides* "B" Griseb.	N, Cly
19.3	*Chloris halophila* Parodi	N, +Cov
19.3	*Drymaria cordata* (L.) Wild. Ex Roem. et Schult.	N
19.3	*Nierembergia andina* Millán	
19.3	*Stipa* sp.	
17.5	*Amicia medicaginea* Griseb.	Sdy
17.5	*Baccharis polifolia* Gris.	
17.5	*Medicago lupulina* L.	N, Cly
17.5	*Senecio pampae* Ling.	+Cov
17.5	*Senna alata* (L.) Rox.	-Phe, Wet, +Cov
15.8	*Cerastrium* sp.	S
15.8	*Cyperus* sp.	+Cov
15.8	*Facelis lasioscarpa* Griseb.	Sdy, +Phe
15.8	*Gutierrezia mandonii* Sch. Bip.	Cly, Dry, -Cov
15.8	*Hypoxis decumbens* Linn.	
15.8	*Balbisia calycina* (Griseb.) A.T. Hunz et Ariza	+Cov

Appendix Continued

F	Spe	class
(%)		
14.0	*Agalinis genistifolia* Cham. & Schltdl.	S
14.0	*Calceolaria fabrisii* Botta & Cabrera	Sdy
14.0	*Eupatorium lorentzii* Hier.	S,Sdy,+Phe
14.0	*Gomphrena celusioides* Mart.	
14.0	*Koeleria* sp.	
12.3	*Apium* sp.	.
12.3	*Dichondra argentea* H. et. B.	Cly, -Cov
12.3	*Gentianella benedictae* (Gilg.) Fabris	S
12.3	*Solanum spegazzinii* Bitter	
12.3	*Sporobolus indicus* (L.) R. Br.	Wet, +Cov
10.5	*Aphanostelma parviflorum* Malme	
10.5	*Botriochloa* sp.	Dry
10.5	*Commelina* aff. *virginica* L.	-Phe, +Cov
10.5	*Evolvulus sericeus* Sw. v. *sericeus*	N
10.5	*Geranium sessiliflorum* Car.	
10.5	*Hieracium neofurcatum* Sleum.	
10.5	*Malaxis padilliana* L.O. Williams	
10.5	*Mutisia acuminata* v. *paucijuga* Gris.	-Phe
10.5	*Opuntia soehrendsii* Britton & Rose	
10.5	*Oxalis bisfracta* Tucrz.	S
8.8	*Anemone decapetala* Ard.	
8.8	*Bulbostylis* sp.	
8.8	*Hieracium dasychaetocomum* Zahn	
8.8	*Hoffmanseggia yaviensis*	
8.8	*Mitracarpus brevis* Schum.	S
8.8	*Paspalum humboldtianum* Flugge	Dry
8.8	*Peperomia peruviana* (Dhlst.) Miq.	
8.8	*Polygala mendocino* Phil.	
8.8	*Stevia lilloi* Rob.	
8.8	*Trichocline auriculata* v. *auriculata* Wedd.	
7.0	*Astragalus* sp.	
7.0	*Calycera pulvinata* Remy.	
7.0	*Conyza serrana* Cabr.	S
7.0	*Conyza spiciformis* Griseb.	S, +Phe
7.0	*Diplachne dubia* (HBK) Scribn.	Dry
7.0	*Eupatorium prassiflolium* Gris.	
7.0	*Gnaphalium jujuyense* Cabrera	
7.0	*Luzula peruviana* Gmeln.	
7.0	*Muhlenbergia peruviana* (P. Beauv.) Steud.	Sdy, +Phe
7.0	*Orchidaceae* sp.	
7.0	*Primulaceae* sp.	
7.0	*Stellaria antoniana* Volponi	-Phe

J. Range Manage.
52:482–488 September 1999

Spotted knapweed, forb, and grass response to 2,4-D and N-fertilizer

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Abstract

Herbicidal control of spotted knapweed (*Centaurea maculosa* Lam.) on rangeland in the western United States has been most effective using residual herbicides, such as picloram (4-amino-3,5,6-trichloropicolinic acid). However, when residual herbicides cause concerns in riparian areas and for non-target forbs, management practices that use herbicides with lower soil persistence need to be developed. The objective of this study was to quantify the interaction between 2,4-D (2,4-Dichlorophenoxyacetic acid, dimethylamine salt) and N-fertilizer on spotted knapweed, other forbs, and grass density and biomass. Five 2,4-D rates (0.0, 0.6, 1.1, 1.6, and 2.2 kg ai ha^{-1}) and 5 N-fertilizer rates (0, 50, 100, 150, and 200 kg ha^{-1}) were applied to 2 spotted knapweed infested rangeland sites in a factorial combination arranged in a randomized-complete-block design during the summer of 1996 in Montana. Spotted knapweed, other forb, and grass density and biomass were measured at peak standing grass crop in 1997 and analyzed using analysis of variance. Spotted knapweed density and biomass at Rock Creek were reduced 50% and 65%, respectively, by 2,4-D of treatments of 1.1 kg ai ha^{-1} or greater. Spotted knapweed biomass was slightly increased by N-fertilizer at 200 kg ha^{-1}. Grass density increased by about 50% when treated with 2,4-D of 1.1 kg ai ha^{-1} or greater N-fertilizer did not affect grass density or biomass. At Hyalite Creek, 2,4-D at 0.6 kg ai ha^{-1} reduced spotted knapweed density by 30%, and rates greater than 0.6 kg ai ha^{-1} reduced it by 75%. Spotted knapweed biomass was reduced by 75% at all herbicide rates tested. N-fertilizer and 2,4-D interacted to increase grass density at Hyalite Creek; however, grass biomass was not affected. At Rock Creek, neither 2,4-D nor N-fertilizer affected forbs. At Hyalite Creek, 2,4-D and N-fertilizer interacted to increase aster (*Aster eatonii* [Gray] Howell) biomass. Death camas (*Zigadenus venenosus* Wats.) biomass was increased by N-fertilizer addition. Combining N-fertilizer with 2,4-D may increase long-term control of spotted knapweed when residual herbicides cannot be used. Application of 2,4-D at the bud stage of spotted knapweed growth will provide some control of spotted knapweed without affecting early season forbs.

Key Words: *Centaurea maculosa*, integrated weed management, maintaining plant diversity, herbicide/fertilizer interaction.

Resumen

El control químico de "Spotted Knapweed" (*Centaurea maculosa* Lam.) en los pastizales del oeste de Estados Unidos ha sido más efectivo con herbicidas residuales como el picloram (ácido 4-amino-3,5,6-trichloropicolonico). Sin embargo, cuando los herbicidas residuales son una preocupación para las áreas ribereñas y las especies que no son el blanco del control, se deben desarrollar practicas que utilicen herbicidas con baja persistencia en el suelo. El objetivo de este estudio fue cuantificar la interacción entre el 2,4-D (ácido 2,4-Dichlorophenoxyacetico, sal de dimetilamina) y la fertilización nitrogenada sobre el "Spotted Knapweed", otras hierbas, y la densidad y biomasa de los pastos. Durante el verano de1996, se evaluaron cinco dosis de 2,4-D (0.0, 0.6, 1.1, 1.6 y 2.2 kg i.a. ha-1) y 5 dosis de fertilización nitrogenada (0, 50, 100, 150,y 200 kg ha^{-1}) en dos sitios de pastizal localizados en Montana e infestados de "Spotted Knapweed". El diseño experimental utilizado fue el de bloques completos al azar en un arreglo factorial. En 1997, cuando la producción de biomasa de los zacates estuvo en su pico máximo, se midió la biomasa y densidad de "spotted Knapweed", otras hierbas y pastos, los datos se analizaron mediante análisis de varianza. En el sitio de Rock Creek, los tratamientos de 2,4-D de 1.1 o más kg i.a. ha^{-1}, redujeron la densidad y biomasa de "Spotted knapweed" en 50% y 65% respectivamente. La biomasa de "Spotted knapweed" se incremento ligeramente con la fertilización nitrogenada de 200 kg ha^{-1}. La densidad de zacate se incrementó en aproximadamente 50% cuando el sitio se trato con 1.1 o más kg i.a. ha^{-1} de 2,4-D. La fertilización nitrogenada no afecto ni la densidad ni la biomasa del pasto. En el sitio de Hyalite Creek, la dosis de 2,4-D de 0.6 o más kg i.a. ha^{-1} redujo la densidad de "Spotted knapweed" en 30%, y dosis mayores de 0.6 kg i.a. ha^{-1} la redujeron en 75%. La biomasa de "Spotted knapweed" se redujo en 75% con todos las dosis de herbicida evaluadas. En Hyalite Creek, la fertilización nitrogenada y el 2,4-D interactuaron para incrementar la densidad del pasto; sin embargo, la biomasa del pasto no fue afectada. En Rock Creek, ni el 2,4-D ni la fertilización nitrogenada afectaron las hierbas. En el sitio de Hyalite Creek, el 2,4-D y la fertilización nitrogenada interactuaron para incrementar la biomasa de "Aster" (*Aster eatonii* [Gray] Howell). La biomasa de "Death camas (*Zigadenus venenosus* Wats) se incremento con la adición de nitrógeno. Cuando herbicidas residuales no pueden ser utilizados, la combinación de fertilización nitrogenada con 2,4-D puede incrementar el control a largo plazo de "Spotted knapweed". La aplicación de 2,4-D en la etapa brotación del "spotted knapweed" proveerá algún control de esta especie sin afectar las hierbas que crecen a inicios de la estación

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Published with the approval of the director, Montana Agricultural Experiment Station, as Journal No. J-5190.

Manuscript Accepted: 13 Dec. 1998.

Spotted knapweed (*Centaurea maculosa* Lam.), an invasive Eurasian weed, has reduced forage production (Watson and Renney 1974, Spoon et al. 1983), increased soil erosion (Lacey et al. 1989), and lowered biodiversity (Tyser and Key 1989) on millions of hectares of rangeland throughout the western United States. This weed has spread to 356 counties in 15 western states and 2 Canadian Provinces during the past 100 years (Lacey et al. 1989, Sheley et al. 1998). The deeply taprooted perennial is an aggressive invader of rangeland dominated by Idaho fescue (*Festuca idahoensis* Elmer), rough fescue (*Festuca scabrella* Torrey ex Hook) and/or bluebunch wheatgrass (*Agropyron spicatum* (Prush) Scribn. & Smith). In Montana alone, where it is the most prevalent rangeland weed, spotted knapweed has infested about 2.2 million ha and has the potential to invade about 50% (20 million ha) of rangeland (Chicoine et al. 1985). Annual cost to the livestock industry in that state exceeds $11 million (Hersch and Leitch 1996).

Picloram (4-amino-3,5,6-trichloropicolinic acid) applied at a rate of 0.28 kg ha^{-1} is most commonly used to control spotted knapweed on rangeland. Picloram residual of 12 to 30 months in the soil (Hamaker et al. 1967, Lacey 1985) and competition from residual perennial grasses (Hubbard 1975, Chicoine 1984, Sheley et al. 1984, Roché 1988) enables picloram to provide about 95% control of spotted knapweed for 2 to 5 years (Davis 1990). However, picloram is a restricted-use herbicide not available to most landowners with small ranchettes, and its use in riparian areas is prohibited because of its long persistence and high solubility.

Where picloram is unacceptable or a herbicide with lower persistence and solubility is preferred, the amine formulation of 2,4-D (2,4-Dichlorophenoxyacetic acid, dimethylamine salt) can provide an effective alternative. This herbicide, applied at 2.2 kg ai ha^{-1}, provides up to 90% control of spotted knapweed the year of application (Dewey et al. 1997). The optimum timing of 2,4-D application is during the active growing period of the target species. On level and accessible land, the cost associated with this treatment is about $25 ha^{-1} (Lacey et al. 1997). On inaccessible areas, such as along rivers and streams, where 2,4-D is often the herbicide of choice, application costs can be as high as $125 ha^{-1}. For long-term control, 2,4-D must be applied annually until the soil seed bank has been depleted. Effective techniques that extend control using 2,4-D need to be developed for this herbicide to be cost effective. The expense associated with annual 2,4-D applications in inaccessible areas suggests that determining techniques which extend the longevity of control is necessary.

Integrating herbicides and fertilizers may have a synergistic effect on providing spotted knapweed control and enhancing grass yield and competitiveness. For example, Sheley and Roche (1982) found that combining picloram (0.28 kg ha^{-1}) with fertilizer (110 kg ha^{-1}; 16(N)-20(P)-0(K)) enhanced grass yield and competitiveness enough to minimize the reinvasion of spotted knapweed in northeastern Washington. More recently, Sheley and Jacobs (1997a) found that picloram plus fertilizer did not interact to affect either spotted knapweed or grass yield. However, fertilizer increased grass yield on the site where smooth bromegrass (*Bromus inermus* Leys.) and timothy (*Phleum pretense* L.) were the dominate grasses, but not on sites dominated by cheatgrass (*Bromus tectorum* L.) or Kentucky bluegrass (*Poa pratensis* L.). They speculated that increased grass yield would increase the duration of spotted knapweed control (Sheley and Jacobs 1997a).

The potential to use combinations of 2,4-D and fertilizer to manage spotted knapweed infested rangeland has not been investigated. Our objective was to quantify the effect of combining 2,4-D and N-fertilizer on spotted knapweed, grass, and other forb density and biomass. We hoped that a mid-summer application of 2,4-D would target spotted knapweed with minimum effect on early season forbs, and N-fertilizer would increase the competitiveness of grass thereby retarding the re-infestation of spotted knapweed. The theoretical basis for this hypothesis is that occupying more niches with a diversity of forbs and competitive grasses more efficiently uses limiting resources and reduces invasibility (Robinson et al. 1995).

Materials and Methods

Study Sites

Field studies were conducted during 1996 and 1997 on 2 sites in western Montana. Site 1 was within a *Festuca scabrella/Agropyron spicatum* habitat type (Mueggler and Stewart 1980) in the flood plain of Rock Creek, 32 km east of Missoula, Mont. (45° 53' 35"N,113° 59' 35"W) on an area previously under cultivation. The soil, a Bigarm gravely loam (loamy-skeletal, mixed, frigid, Typic Eutrochrepts) had 0 slope and an elevation of 1,160 m. Annual precipitation ranges from 406 to 457 mm and the frost-free period ranges from 70 to 90 days. Dominated by spotted knapweed, the site appeared to be in an advanced stage of invasion. Spotted knapweed density was high (140 plants m^{-2}, SD=52), the residual grass was suppressed, and there were few species of forbs. The suppressed grass understory consisted of scattered Kentucky bluegrass with small patches of smooth bromegrass. Other forbs consisted of low densities of yarrow (*Achillia millefolium* L.), sulfur cinquefoil (*Potentilla recta* L.), and silvery cinquefoil (*Potentilla argentea* L.).

Site 2 was on pasture land within the flood plain of Hyalite Creek 15 km west of Bozeman, Mont. (45° 36' 26"N, 111° 5'36"W). The area was within a *Festuca idahoensis/Agropyron spicatum* habitat type (Mueggler and Stewart 1980). The soil, a complex consisting of 70% Beaverton cobbly loam (loamy-skeletal over sandy or sandy-skeletal, mixed, Typic Argiborolls) and 30% Hyalite loam (fine-loamy, mixed, Typic Argiborolls) had 0 slope and an elevation of 1,340 m. Annual precipitation ranges from 381 to 483 mm and the frost-free period ranges from 90 to 110 days. This site appeared to be in the early stages of spotted knapweed invasion because it was dominated by Idaho fescue and native forbs with scattered spotted knapweed plants. Mean spotted knapweed density was 35 plants m^{-2} (SD=11). Grass species present were Idaho fescue, bluebunch wheatgrass, Kentucky bluegrass, and smooth bromegrass. Other forbs that were present are listed in Table 1.

Experimental Design

Twenty-five treatments (5 herbicide rates, 5 fertilizer rates) were applied to 2 m by 4 m plots and factorially arranged

Table 1. List of forbs sampled at Site 2, Hyalite Creek.

Common name	Scientific name
Annual Forbs	
Large-flowered collomia	*Collomia grandiflora* Dougl.
Narrow-leafed collomia	*Collomia linearis* Nutt.
Indian lettuce	*Montia linearis* (Dougl.) Green
Shining chickweed	*Stellaria nitens* Nutt.
Perennial Forbs	
Yarrow	*Achillea millefolium* L.
Ballhead sandwort	*Arenaria congesta* Null.
Arnica	*Arnica longifolia* D.C. Eat.
Prairie sage	*Artemisia ludoviciana* Nutt.
Aster	*Aster eatonii* (Gray) Howell
Arrowleaf balsamroot	*Balsamorhiza sagittata* (Pursh) Nutt.
Larkspur	*Delphinium bicolor* Nutt.
Glacier lily	*Erythronium grandiflorum* Prush
Desert parsley	*Lomatium macrocarpa* (Nutt.) Coult.& Rose
Silvery lupine	*Lupinus argenteus* Pursh
Manyflowered phlox	*Phlox multiflora* A. Nels.
Smallflowered pennycress	*Thlaspi parviflorum* Nels.
Salsify	*Tragopogon dubious* Scop.
Death camas	*Zigadenus venenosus* Wats.

in a randomized-complete-block design. The experiment was replicated 4 times at each site. In the summer of 1996, 2,4-D rates of 0.0, 0.1, 1.1, 1.6, and 2.2 kg ai ha^{-1} were applied using a 4 nozzle backpack sprayer delivering 130 liter ha^{-1} spray solution. A granular fertilizer, formulated as 32-0-0-0 (NPKS), was broadcast at rates of 0, 163, 326, 490, and 652 kg ha^{-1} (0, 50, 100, 150, and 200 kg ha^{-1} N) using a hand-cyclone applicator. The Rock Creek site was treated on 2 June 1996. Air temperature, soil temperature (surface), and relative humidity were 15.5°C, 21°C, and 78%, respectively, at the time of application. Winds were calm (<5 km hr^{-1}). The Hyalite Creek site was treated on 1 July 1996. Air temperature, soil temperature (surface), and relative humidity were 17.5°C, 21°C, and 50%, respectively at the time of application. Winds ranged from 0 to 6 km hr^{-1}. Spotted knapweed was in the bolt and bud growth stage at Rock Creek and Hyalite Creek, respectively, while other forbs were in various stages of senescence.

Sampling

Density and biomass of spotted knapweed, grass and other forbs were sampled at peak standing crop (July) 1997. Densities were counted in a 0.1 m^2 (2 X 5 dm) frame (Daubenmire 1970) randomly placed within each plot. Grass species, Kentucky bluegrass and smooth bromegrass at Rock Creek and Idaho fescue, bluebunch wheatgrass, Kentucky bluegrass, and smooth bromegrass at Hyalite Creek, were counted by tiller. A 0.42 m^2 hoop was then placed to encircle the frame and biomass standing crop was harvested by species. Samples were dried at 60°C to constant weight and weighed.

Data Analysis

Data were first analyzed with multiple linear regression (least squares) models using 2,4-D and N-fertilizer as independent variables. Scatterplots of the residual versus the standardized predicted values indicated that most of the data did not fit a linear model. Therefore, all data were analyzed using standard analysis of variance procedures. The 2 sites were analyzed separately because the original species compositions were different. The model included 2,4-D, N-fertilizer, and 2,4-D x N-fertilizer. When a significant ($P \leq 0.05$) F-test was observed, differences among means were tested using protected least significant differences (LSD) procedures (Peterson 1985). Forbs were analyzed as total forbs, total annual forbs, total perennial forbs, and by species.

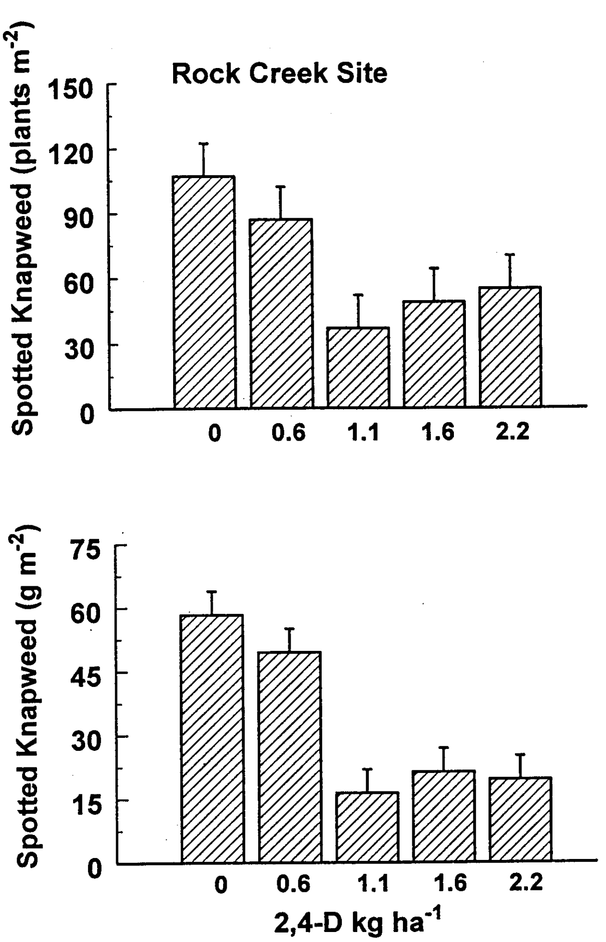

Fig. 1. Effect of 2,4-D on spotted knapweed density (plants m^{-2}) and biomass (g m^{-2}) at Rock Creek. Error bars represent least significant differences (0.05).

Results

Two, 4-D and N-fertilizer did not interact to affect spotted knapweed density or biomass (Table 2, Table 3). On both sites, 2,4-D reduced spotted knapweed density and biomass the second season after treatment; however there were rate differences between sites. At Rock Creek, 2,4-D applied at 1.1 kg ai ha^{-1} or greater reduced spotted knapweed density by about 50% and biomass by 65% (Fig.1). When 2,4-D was applied at 0.6 kg ai ha^{-1} spotted knapweed density and biomass were similar to that of the control. At Hyalite Creek, spotted knapweed density was reduced by about 37% with 0.6 kg ai ha^{-1} of 2,4-D (Fig. 2). Two,4-D applied at 1.1 kg ai ha^{-1} and greater reduced spotted knapweed density by about 75%. All nonzero rates reduced spotted knapweed biomass by 75%. N-fertilizer did not affect spotted knapweed density or biomass at either site

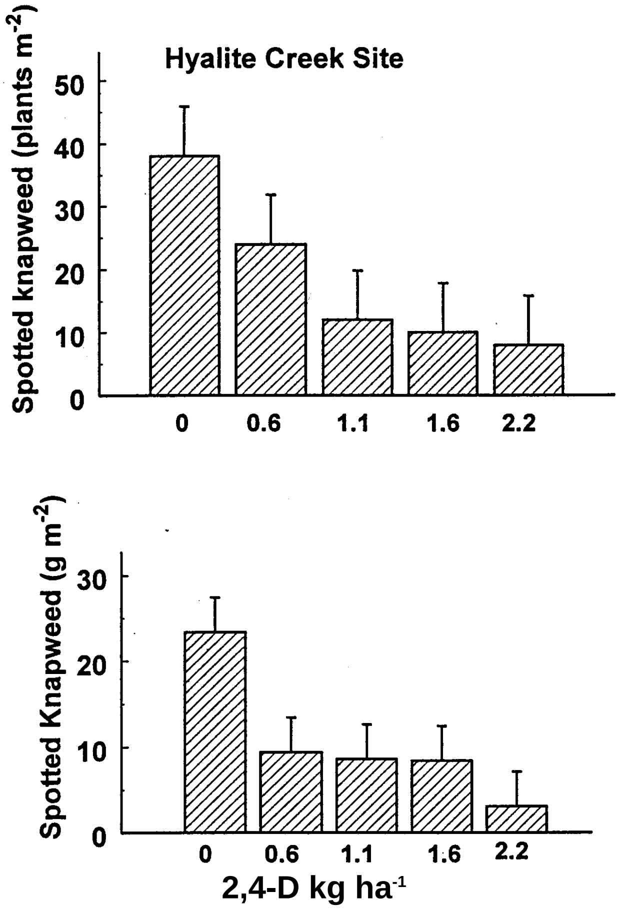

Fig. 2. Effect of 2,4-D on spotted knapweed density (plants m^{-2}) and biomass (g m^{-2}) at Hyalite Creek. Error bars represent least significant differences (0.05).

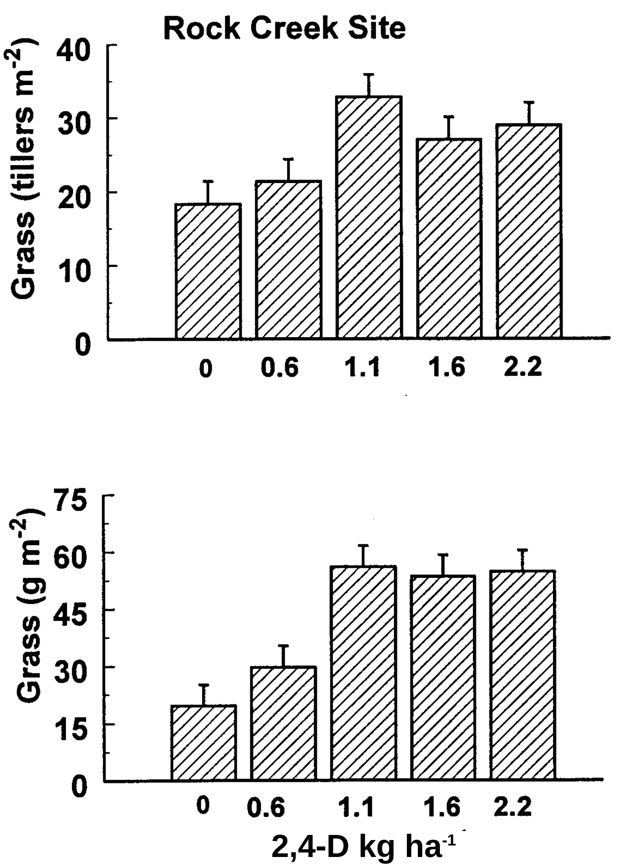

Fig. 3. Effect of 2,4-D on grass density (tillers m^{-2}) and biomass (g m^{-2}) at Rock Creek. Error bars represent least significant differences (0.05).

(Table 2, Table 3).

Combinations of 2,4-D and N-fertilizer did not interact to affect grass density or biomass at Rock Creek (Table 2). In addition, grass did not respond to N-fertilizer applications. Grass density and biomass did increase as a result of 2,4-D applications (Table 2, Fig. 3). Grass density increased slightly with 2,4-D applied at 1.1 kg ai ha^{-1} or greater. Grass biomass increased 40% compared to the control when 2,4-D was applied at 0.6 kg ai ha^{-1} and 65% compared to the control when 2,4-D was applied at 1.1 kg ai ha^{-1} or more.

At Hyalite Creek, grass biomass was not affected by either 2,4-D or N-fertilizer, however, the combination interacted to increase grass density (Table 3). Grass density increased with 2,4-D application when no fertilizer was applied (Fig. 4). When no 2,4-D was applied, N-fertilizer did not increase grass density. When 2,4-D was applied at 1.1 kg ai ha^{-1} or greater, adding 150 or 200 kg ha^{-1} N-fertilizer caused an increase in grass density.

Forb density and biomass were unaffected by 2,4-D or N-fertilizer at Rock Creek (Table 2). At Hyalite Creek, forb density was also unaffected by 2,4-D or N-fertilizer, but treatments interacted to affect aster biomass and fertilizer increased death camas biomass (Table 3). Aster biomass was unaffected by 2,4-D or N-fertilizer when applied alone, however, when 200 kg ha^{-1} of N-fertilizer was applied in combination with 2.2 kg ai ha^{-1}, aster biomass increased 10-fold (Fig. 5). Death camas biomass was increased about 3-fold by 50 kg ha^{-1} N-fertilizer addition (Fig. 6).

Discussion

It is becoming increasingly clear that the response of a

Table 2. The significance probability associated with the F statistic ($Pr \leq F$), generated from analysis of variance, for each species at the Rock Creek site.

	Density			Biomass		
Species	2,4-D	N	2,4-D*N	2,4-D	N	2,4-D*N
Knapweed	<0.01	0.98	0.63	<0.01	0.07	0.29
Grass	<0.01	0.64	0.76	<0.01	0.57	0.99
All Forbs	0.62	0.23	0.89	0.55	0.35	0.83

Table 3. The significance probability associated with the F statistic (Pr≤F), generated from analysis of variance, for each species at the Hyalite Creek site.

	Density			Biomass		
Species	2,4-D	N	2,4-D*N	2,4-D	N	2,4-D*N
Knapweed	<0.01	0.39	0.59	0.01	0.56	0.83
Grass	<0.01	<0.01	0.02	0.36	0.23	0.60
All Forbs	0.92	0.19	0.19	0.88	0.26	0.66
Ann. Forbs	0.55	0.27	0.19	0.58	0.31	0.47
Collomia g.	0.91	0.45	0.29	0.59	0.41	0.74
Collomia l.	0.50	0.15	0.17	0.51	0.99	0.32
Montia	0.40	0.13	0.19	0.78	0.41	0.44
Stellaria	0.78	0.71	0.53	0.63	0.77	0.58
Per. Forbs	0.89	0.88	0.49	0.46	0.60	0.87
Yarrow	0.64	0.76	0.18	0.47	0.79	0.57
Sandwort	0.62	0.72	0.23	0.39	0.81	0.38
Arnica	0.70	0.68	0.63	0.48	0.34	0.70
Prairie sage	0.65	0.84	0.56	0.61	0.84	0.54
Aster	0.91	0.26	0.63	0.02	<0.01	0.03
Balsamroot	0.18	0.05	0.11	0.53	0.36	0.64
Larkspur	0.91	0.64	0.80	0.57	0.60	0.05
Glacier lily	0.06	0.47	0.14	0.27	0.18	0.47
Desert parsley	0.44	0.34	0.30	0.34	0.68	0.67
Lupine	0.65	0.37	0.70	0.27	0.46	0.67
Phlox	0.18	0.29	0.15	0.94	0.42	0.70
Pennycress	0.46	0.14	0.82	0.34	0.66	0.57
Salsify	0.42	0.53	0.28	0.56	0.61	0.55
Camas	0.67	0.93	0.96	0.61	0.04	0.10

plant community and the decision to use herbicides are dependent upon the composition and abundance of the residual species in the understory prior to application (Sheley et al. 1996, Sheley and Jacobs 1997a). As expected, the response of the plant community to 2,4-D and N-fertilizer combinations was dependent on the initial composition of the plant community. On the site dominated by spotted knapweed with a depleted grass and forb understory, only 2,4-D affected spotted knapweed, which resulted in a corresponding increase in grass density and biomass. At this site, we believe the release of grass from spotted knapweed suppression masked any effect the addition of N-fertilizer may have had. On the Idaho fescue-dominated site with a diverse forb component, 2,4-D and N-fertilizer interacted to increase grass density. Increasing grass density relative to spotted knapweed density has been shown to shift the competitive advantage from spotted knapweed to grass (Jacobs et al. 1996, Sheley and Jacobs 1997b).

The current recommended rate for controlling spotted knapweed using 2,4-D is 2.2 kg ai ha^{-1} applied annually (Dewey et al. 1997). Our results show that 1.1 kg ai ha^{-1} 2,4-D applied at bolt or bud stage had the same level of spotted knapweed control as higher rates the second season after treatment. N-fertilizer rates of 150 kg ha^{-1} or greater increased grass density when 2,4-D was applied. These results suggest that 2,4-D applied at 1.1 kg ai ha^{-1} applied in combination with 150 kg ha^{-1} N-fertilizer should provide the optimum long-term control of spotted knapweed where persistent herbicides are not used.

Optimum rates of 2,4-D and/or 2,4-D plus N-fertilizer controlled spotted knapweed and increased grass yield without affecting other forbs. Plant diversity has been shown to improve plant community recovery from stress, such as drought (Tilman 1996) and increase resistance to plant invasion (Sheley et al. 1996, Tilman 1997). Jacobs and Sheley (1998a) found that northern sweetvetch (*Hedysarum boreale* Nutt.), a native, taprooted forb, when seeded with bluebunch wheatgrass reduced the competitiveness of spotted knapweed, supporting the theory that a diverse plant community is more resistant to weed invasion. Long-term control using repeated applications of picloram reduces forb diversity (Rice et al. 1997). Many native forbs that

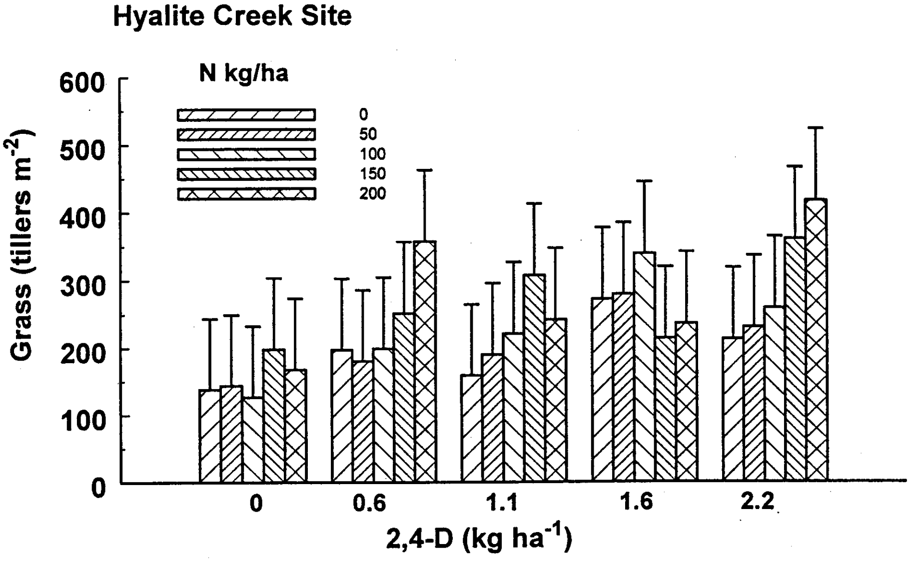

Fig. 4. Effect of 2,4-D and N-fertilizer combinations on grass density (tillers m^{-2}) at Hyalite Creek. Error bars represent least significant differences (0.05).

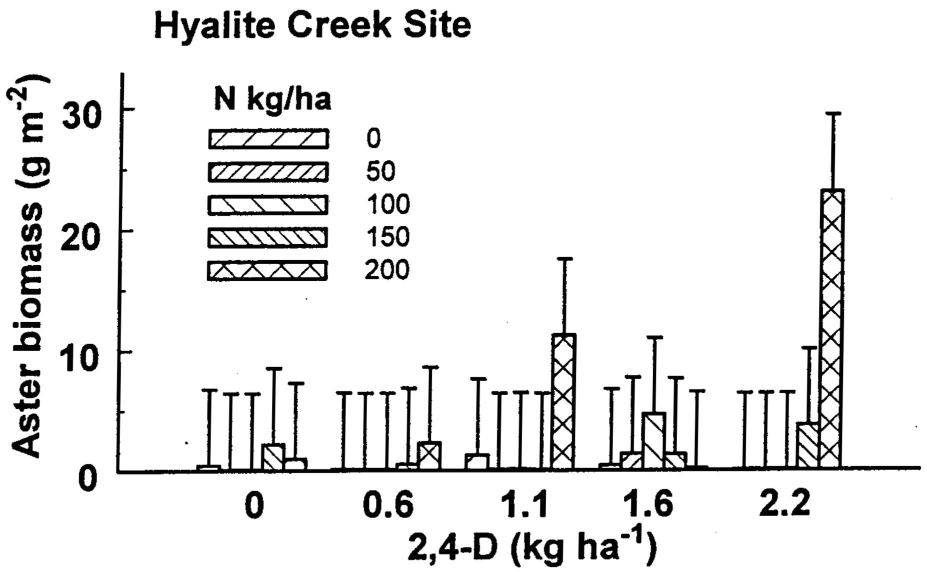

Fig. 5. Effect of 2,4-D and N-fertilizer combinations on aster biomass (g m^{-2}), at Hyalite Creek. Error bars represent least significant differences (0.05).

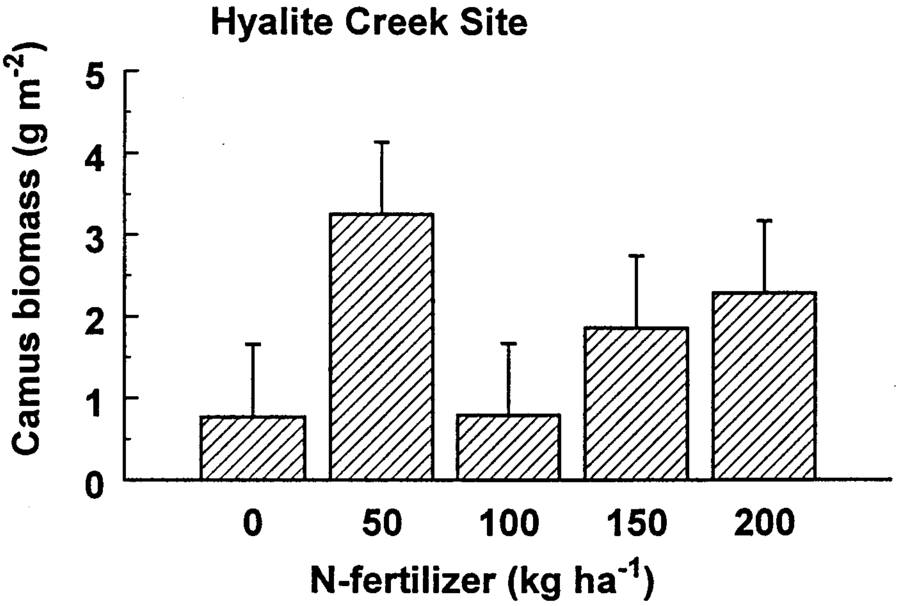

Fig. 6. Effect of N-fertilizer on death camas biomass (g m^{-2}), at Hyalite Creek. Error bars represent least significant differences (0.05).

emerge and mature early in the growing season are affected by picloram residue. Spotted knapweed remains actively growing throughout much of the summer (Jacobs and Sheley 1998b) and can be controlled with non-residual herbicide application at the bud stage of growth without affecting spring and early summer forbs. We believe that this creates a phenological and temporal opportunity to maximize herbicidal effects on spotted knapweed, while minimizing exposure to desirable native forbs. Furthermore, the lack of soil persistence of 2,4-D should limit long-term effects. Our study suggests that in areas with substantial residual native plant communities, 2,4-D plus N-fertilizer applied in mid-summer can effectively control spotted knapweed, and increase grass density over that of 2,4-D alone without reducing native forbs.

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Prescribed fire effects on biological control of leafy spurge

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Abstract

The flea beetle, *Aphthona nigriscutis* Foudras, is a potentially useful agent for biological control of leafy spurge (*Euphorbia esula* L.) in grasslands devoted to wildlife conservation. However, effects of other grassland management practices on the persistence and dynamics of flea beetle populations are not well understood. We conducted small plot tests to evaluate 1) the effect of prerelease burning on establishment of *A. nigriscutis* colonies, and 2) the ability of established *A. nigriscutis* colonies to survive prescribed fire. More colonies established on plots that were burned prior to beetle release (83% establishment) than on unburned plots (37% establishment), possibly due to litter reduction and baring of the soil surface. However, most colonies established with the aid of fire did not survive past the first generation unless the habitat was otherwise suitable for the species, and we conclude that the primary benefit of prerelease burning is increased recruitment of *A. nigriscutis* during the first few generations. Established colonies were not harmed by burns in October and May. Both spring and fall burns resulted in an increase in leafy spurge stem density during the first growing season, but stem density declined to the preburn level by the second growing season.

Key Words: *Euphorbia esula*, northern Great Plains, *Aphthona nigriscutis*, flea beetles

Resumen

En pastizales dedicados a la conservación de fauna silvestre, el "Flea beetle" (*Aphthona nigriscutis* Foudras) es un agente potencialmente útil para el control del "Leafy spurge". Sin embargo, los efectos de otras practicas de manejo de pastizales en la persistencia y dinámica del "Flea beetle" no son bien entendidos. Se condujeron pruebas en parcelas pequeñas para evaluar: 1) el efecto de la quema antes de la liberación del insecto en el establecimiento de colonias de *A. Nigriscutis* y 2) la capacidad de las colonias establecidas de *A. Nigriscutis* para sobrevivir al fuego prescrito. Se establecieron mas colonias (83% de establecimiento) en las parcelas que se quemaron antes de la liberación de A. Nigriscutis que en las parcelas sin quema (37%), posiblemente debido a la reducción de mantillo y la desnudez de la superficie del suelo. Sin embargo, muchas de las colonias establecidas con ayuda del fuego no sobrevivieron pasada la primer generación, a menos que el hábitat fuera adecuado para la especie. Concluimos que el beneficio primario de la quema de preliberación es el incremento en el reclutamiento de *A. nigriscutis* durante las primeras generaciones. Las colonias establecidas no fueron dañadas por las quemas de Mayo y Octubre. Las quemas de primavera y otoño incrementaron de la densidad de tallos de "Leafy spurge" durante la primera estación de crecimiento, sin embargo, en la segunda estación de crecimiento, la densidad de tallos disminuyó al nivel existente antes de la quema.

Leafy spurge (*Euphorbia esula* L.) is a major noxious weed on wildlife refuges, parks, waterfowl management areas, and other grasslands dedicated to biological conservation throughout the northern Great Plains (Wallace et al. 1992). Although studies are just beginning to document ecological impacts of leafy spurge (Belcher and Wilson 1989, Trammell and Butler 1995), the species' ability to form nearly monotypic stands (Watson 1985) clearly threatens native biodiversity.

Conventional chemical and physical control of leafy spurge is seldom practical on conservation lands because of cost (Messersmith and Lym 1983), risks to the native flora, or conflicts with the needs of wildlife. Biological control may thus be a preferred approach to control of leafy spurge on conservation lands, provided the control agent(s) is compatible with practices used to manage grassland habitats. Of primary concern is prescribed burning, which is widely used to manipulate prairie vegetation for the benefit of native communities (Higgins et al. 1989).

Flea beetles of the genus *Aphthona* (Coleoptera: Chrysomelidae) appear to be the most promising of the insects currently approved for biocontrol of leafy spurge in the U.S. (Rees and Spencer 1991). All but 1 approved *Aphthona* species are univoltine. Adults of univoltine species begin to emerge in mid- to late June and lay eggs in the soil near leafy spurge crowns until early September. Although adults feed on leafy spurge foliage, control is exerted by the larvae, which feed on leafy spurge roots. Larvae overwinter in the soil and pupate in late spring to early summer.

The univoltine *A. nigriscutis* Foudras appears generally adapted to upland soil types and moisture conditions on many wildlife management areas in the northern Great Plains (Rees

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The authors thank N. Spencer, USDA-ARS, for providing beetles and assistance in study design. N. Spencer, R. Carlson, D. Larson, and G. Sargeant provided critical reviews of the draft manuscript.

Manuscript accepted 11 Nov. 1998.

and Spencer 1991). However, possibly because the litter layer interferes with reproduction, the species is difficult to establish in the dense, mixed stands of leafy spurge and grass that often prevail on these lands (N.R. Spencer, pers. comm).

The first objective of this study was to determine whether burning to remove the litter layer would facilitate establishment of *A. nigriscutis*. We tested both fall and spring burns to assess influence of burn season on establishment. This phase of the study also provided opportunity to assess initial combined effects of fire and beetle populations on leafy spurge stem density. Our second objective was to determine the ability of established colonies of *A. nigriscutis* to survive prescribed burns conducted during the early fall and late spring.

Methods

General

The study was conducted on U.S. Fish and Wildlife Service lands in south central and southeastern North Dakota. Study areas consisted of Arrowwood National Wildlife Refuge, Thiesen Marsh Waterfowl Production Area (WPA), and Walsh WPA in Stutsman Co.; Storhoff WPA in Barnes Co.; and Kemmer WPA in Cass Co. None of the study areas had been burned since at least 1985.

On each study area, we delineated 2 blocks of six, 11-m diameter treatment plots. Blocks within a study area were separated by a minimum of 300 m, and outer perimeters of adjoining plots within a block were separated by a minimum of 3 m. Plots within a block were visually selected for similar topography, elevation, exposure, and vegetative cover, and plot centers were visually placed at the highest density of spurge. Each of 6 treatments was randomly assigned to 1 plot within each block. Treatments consisted of: beetles only (beetles released, no burning); fall preburn (burned in fall preceding beetle release); spring preburn (burned in spring preceding beetle release); fall postburn (burned in fall after beetles were confirmed to have established); spring postburn (burned in spring after beetles were confirmed to have established); and control (unburned, no beetles released).

We established 4 equally spaced permanent transects radiating from the center to the perimeter of each plot. In July, 1993, we estimated leafy spurge height and stem density, depth of litter layer, and percent cover of leafy spurge, grasses, shrubs, forbs, and bare ground (Daubenmire 1959) at distances of 1, 3, and 5 m from the plot center on each of the transects. Leafy spurge stem density-was estimated again at the same sampling points in July 1994 and 1995.

We used analysis of variance (ANOVA) to examine vegetation data collected in 1993. Our ANOVA model was a split-plot in a randomized block design. Study area by block combinations were considered random blocks, with plots being whole-units and distance from the center of the plot the subunit (Steel and Torrie 1980). Within distance classes, data from each plot were averaged across the transects. The general linear models procedure (PROC GLM) of SAS (SAS Institute Inc., 1989b) was used to conduct ANOVAs throughout this study. Exploratory distribution plots of all response variables did not indicate any violations of normality assumption; therefore all analyses were conducted in original units of measurement. Fisher's LSD procedure was used for multiple comparisons (Milliken and Johnson 1984). Reported means are least-squares means (SAS Institute, Inc. 1989b) unless stated otherwise. Statistical tests were considered significant at the 0.05 level.

Experiment 1: Effects of prerelease burning on establishment

Fall-preburn and spring-preburn plots were burned on 14–21 Oct. 1993 and 5–11 May 1994, respectively. Spurge was dormant during fall burns, but actively growing (8–30 cm tall) during spring burns. Burns removed 95–100% (visual estimate) of standing vegetation and litter on all plots.

On 27–29 June 1994, we released 150 *A. nigriscutis* at the center of each fall- and spring-preburn, fall- and spring-postburn, and beetle-only plot. Beetles used in the study were collected by the USDA Agricultural Research Station in Sidney, Mont., from the "Rugg" insectary (Glendive, Mont.) and were refrigerated until their release within 5 days after capture.

Beginning 13 June 1995, shortly after beetles began to emerge in *A. nigriscutis* insectaries at Northern Prairie Wildlife Research Center (Stutsman Co., N.D.), plots were swept once for beetles on each of 3 days at intervals of about 1 week during suitable weather (sunshine, dry vegetation, temperature ≥25°C, wind ≤17 km/hr). A standard sweep sample consisted of 5 sweeps through the upper 25–30 cm of vegetation with a 39-cm diameter sweep net on each of 5 equally spaced transects from the perimeter to the center of the plot, for a total of 25 sweeps. Captured beetles were counted and released immediately at the center of the plot. The greatest number of beetles captured on a plot in a standard sample during the 3 days was used as a population index for that plot.

In 1996, all plots on which beetles were collected in 1995, except those burned in experiment 2 (see below), were again swept for beetles 3 times beginning on 18 June to assess size of the second generation. Between 8–11 July 1996, a single auxiliary sample, consisting of 45–50 sweeps in a spiral pattern from the center to the edge of the plot, was taken on plots on which no beetles were found in standard sweep net samples in 1996. An auxiliary sample was also taken on plots where no beetles had been found in 1995 on the Storhoff, Walsh, Arrowwood, and Kemmer study areas.

Frequency of occurrence (number of plots with beetles established vs not established) was analyzed with chi-square tests of homogeneity (Dowdy and Weardon 1983) in 2-way tables. The categorical data modeling procedure (PROC CATMOD) of SAS (SAS Institute, Inc. 1989a) was used to conduct chi-square tests. ANOVA in a randomized block design (Steel and Torrie 1980) was used to assess the effects of treatments on beetle population index in 1995 because distance from center of plot was not taken into account for these data. Again, study area by block combinations were considered random blocks. We used split plot ANOVA to test for differences in vegetation between plots in which beetles became established and plots in which they did not. Each study plot was treated as a whole-plot. Observations within whole-plots were assigned to sub-plots according to their distance from the plot center. To examine joint treatment effects of fire and beetles on leafy spurge stem density from 1993 to 1994 and 1993 to 1995, ANOVA was also used, with the model being as described for pre-treatment vegetation data above.

Experiment 2: Effect of burning on established colonies

Because few colonies were found on the postburn and beetle only plots in 1995, the study was modified to test the effect of burning on established colonies. We selected the 12 plots with the greatest indicated *Aphthona* populations on the Storhoff, Kemmer, and Arrowwood study areas and randomly assigned 1 of 3 treatments (fall-burn, spring-burn, and unburned reference) to each of 4 plots. Most of these 12 plots were fall- and spring-preburn plots. Burns were conducted 11–23 Oct 1995 on the fall-burn plots and 13–16 May 1996 on the spring-burn plots; spurge phenology and results of burns were similar to those in 1993–94. Beginning on 6 June 1996, we swept all plots 3 times as described above. Changes in beetle population indexes from 1995 to 1996 by treatment were analyzed with ANOVA in a 1-way design, with plots nested within burn or reference groups.

Results

General

Herbicide drift from adjoining cropland top-killed varying percentages of leafy spurge on all Walsh block 1 ("Walsh-1") plots in June 1994. The fall-postburn plot on Storhoff-1 was lost to vandalism in the winter 1994–95. Data from these plots were excluded from all analyses.

Table 2. Mean initial vegetative conditions at distances of 1, 3, and 5 m from plot center. Values are least-squares means.

Distance	Leafy Spurge Density	Leafy Spurge Height	Leafy Spurge Cover	Grass Cover	Forb Cover	Bare Ground	Litter Depth
(m)	(stems m^{-2})	(cm)	(%)	(%)	(%)	(%)	(cm)
1	193^b	40^b	69^c	34^a	2.7^a	3.4^a	4.8^a
2	190^b	39^{ab}	64^b	36^a	2.8^a	5.6^a	4.8^a
3	163^a	38^a	60^a	39^b	2.7^a	3.9^a	4.7^a
SE[1]	6.4	0.4	1.2	1.1	0.1	0.7	0.2

[1] Pooled standard error for variable.

[a-b] Means within a column with different superscripts are different ($p<0.05$).

No pretreatment differences were detected among treatments for any of the vegetation variables measured in 1993 ($p>0.11$). However, differences ($p<0.01$) occurred among blocks for percent spurge cover, percent grass cover, percent forb cover, percent bare ground, and litter depth (Table 1). Leafy spurge stem density, height, and percent cover decreased, and grass percent cover increased, with increasing distance from center of plot ($p<0.01$, Table 2). No interactions were found between treatment and distance ($p>0.11$) except for spurge height ($p=0.03$).

Experiment 1

In 1995 we collected ≥1 beetle in standard sweep samples on 8 of 9 fall-preburn and 7 of 9 spring-preburn plots, compared to only 10 of 26 unburned plots. The proportion of plots on which ≥1 beetle was captured (i.e. "colonized plots") did not differ between fall-preburn and spring-preburn plots ($p=0.52$), but was higher ($p<0.01$) on burned (fall-preburn and spring-preburn combined) than on unburned plots.

In 1995, mean population indexes (SE) were 1.9 (1.4), 9.9 (2.3), and 10.2 (2.3) for unburned, fall-preburn, and spring-preburn plots, respectively. Population indexes did not differ between the spring- and fall-preburn treatments ($p=0.92$), but were higher on burned than unburned plots ($p<0.01$). Comparison of treatment effects on population indexes using only colonized plots indicated the presence of larger populations on burned than unburned plots, with arithmetic means (SE) of 4.7 (3.3), 11.1 (3.0), and 13.1 (3.6) for unburned, fall-preburn, and spring-preburn plots, respectively.

The proportion of plots colonized varied among blocks (Table 3), suggesting that conditions were more suitable for beetles on some blocks than on others. Comparison of 1993 vegetation on colonized vs uncolonized plots using only the unburned plots revealed differences in litter depth (means of 3.6 cm colonized, 5.1 cm uncolonized, $p=0.05$) and percent bare ground (5.7% colonized, 3.0% uncolonized, $p=0.02$). No other differences in vegetation were found between colonized and uncolonized plots ($p>0.10$). Comparison of Tables 1 and 3 suggests a positive correspondence between overall colonization success and mean percent bare ground on the 9 blocks; bare ground averaged 5.5–9.9% on blocks Storhoff-2 and Kemmer-2, where beetles established on all plots, 3.7–4.9% on Arrowwood-1, Storhoff-1, and Walsh-2, where some unburned plots and all of the burned plots were colonized, and 2.5–3.3% on the remaining blocks, where none of the unburned, and only some of the burned, plots were colonized. No such relationship was apparent for litter depth.

Eight of 25 colonized plots were burned in fall 1995 or spring 1996 to evaluate effects of burning on established colonies (see experiment 2). Among the remaining 17 colonized plots that were not burned for experiment 2, standard sweep samples in 1996 indicated that populations had increased

Table 1. Mean initial vegetative conditions on 9 treatment blocks. Values are least-squares means.

Block	Leafy Spurge Density (stems m^{-2})	Leafy Spurge Height (cm)	Leafy Spurge Cover (%)	Grass Cover (%)	Forb Cover (%)	Bare Ground (%)	Litter Depth (cm)
A1[1]	173^a	35^a	59^{ab}	29^{ab}	2.7^{ab}	4.9^a	3.5^{ab}
A2	269^a	42^a	79^c	33^a	2.5^a	2.7^a	4.7^{ab}
K1	148^a	39^a	60^{ab}	35^b	2.7^{ab}	3.3^a	4.6^{ab}
K2	222^a	35^a	68^{bc}	44^b	2.5^a	9.9^b	2.8^a
S1	142^a	41^a	69^{bc}	46^{bc}	3.2^{bc}	3.7^a	5.1^{bc}
S2	203^a	37^a	60^b	34^b	3.7^c	5.5^a	5.5^{bc}
T1	148^a	42^a	65^{abc}	41^{bc}	2.5^a	2.7^a	6.9^c
T2	129^a	42^a	52^a	53^c	2.5^a	2.5^a	6.2^c
W2	211^a	39^a	69^{bc}	14^a	2.5^a	3.7^a	3.4^{ab}
SE[2]	34	2	5	7	0.2	1.1	0.8

[1] Block names: A=Arrowwood NWR, K=Kemmer WPA, S= Storhoff WPA, T=Thiesen WPA, W=Walsh WPA; numbers indicate block number.

[2] Pooled standard error for variable.

[a–c] Means within a column with different superscrpts are different ($p<0.05$).

Table 3. Colony establishment by block and treatment. Block designations as in Table 1.

Block	Unburned	Burned
	(no. colonized/n. plots)	
K2	3/3	2/2
S2	3/3	2/2
A1	2/3	2/2
S1	1/2	2/2
W2	1/3	2/2
T2	0/3	1/2
K1	0/3	1/2
A2	0/3	1/2
T1	0/3	1/2

or remained constant on 5, and decreased or gone extinct on 6, of the preburn plots. Similar results were noted on the unburned plots, with 3 populations increasing or stable and 3 declining or extinct.

Auxiliary samples in 1996 revealed presence of small populations (1–7 captures/plot) on 4 of 8 plots where beetles were captured in standard sweep samples in 1995 but not in 1996. No beetles were collected in auxiliary samples in 1996 on any of the plots where no beetles were detected in standard sweep samples in 1995.

Joint treatment effects of fire and beetles on leafy spurge stem density from 1993 to 1994 and 1993 to 1995 are compared in Table 4, first using all plots, and then using only plots on which beetles were detected in both 1995 and 1996. Both data sets indicate that stem density increased more ($p<0.01$) on the burned than on the unburned plots in 1994, but that the net change from 1993 to 1995 did not differ between treatments ($p>0.30$). Distance from plot center had no effect on change in stem density, and no distance x treatment interaction was found in any of the comparisons ($p>0.29$).

Experiment 2

Beetles were collected in standard sweep samples in 1996 on all 12 plots used to evaluate effects of fire on established colonies. Populations increased on 10 plots and decreased on 2 plots (1 reference and 1 spring-burn). Mean increase in number (SE) of beetles captured from 1995 to 1996 was 51.5 (33.3), 70.8 (33.3), and 36.8 (33.3) for unburned, fall-burn, and spring-burn plots, respectively. Treatment differences were not significant ($p=0.77$).

Discussion

Prerelease fall or spring burning enhances colonization by *A. nigriscutis*. Although results of auxiliary samples indicate that standard sweep samples may have failed to detect some small populations in 1995, none was sufficiently established to persist into the second year.

Benefits of burning may be short-lived if habitat is unsuitable for other reasons. Beetles established on only 1 of 15 unburned plots on Walsh-2, Thiesen-1 and -2, Kemmer-1, and Arrowwood-2, (Table 3) suggesting that unburned habitat on these blocks was unsuitable for *A. nigriscutis*. Five of 7 colonies detected on preburned plots on those blocks in 1995 failed to survive into 1996. In contrast, on Kemmer-2, Storhoff-2, and Arrowwood-1, where beetles established on 8 of 9 unburned plots, all colonies on preburned plots persisted into 1996.

The positive effect of bare ground and the negative effect of litter depth on colonization suggested by our data support the hypothesis (N.R. Spencer, pers. comm.) that *A. nigriscutis* may be limited in part by factors that impede access to the soil surface. If litter reduction and/or exposure of bare soil are the primary mechanisms facilitating establishment on burned sites, rapid litter buildup and plant regeneration following a burn may cause benefits to be only transitory even in relatively good *A. nigriscutis* habitat. However, as long as the habitat is otherwise suitable, increased early recruitment from prerelease burning should ultimately enhance control.

One possible objection to prerelease burning concerns potential effects of fire on leafy spurge. Wolters et al.(1994) reported increased leafy spurge stem density in the first growing season following spring (4 May), but not fall (19 Sept.), burns in southwestern North Dakota. Thus, a spring burn followed by an unsuccessful beetle release might leave the manager with an even denser stand of leafy spurge. We observed significant increases in stem density during the first growing season after both spring and fall burns (Table 4). However, the increases did not persist into the second growing season.

It is unlikely that beetles caused the observed decline in stem density on burned plots from 1994 to 1995. Populations were low on most plots in 1995, and stem counts declined uniformly throughout each plot, whereas beetles were concentrated at the plot center. Although Wolters et al.(1994) concluded that fire reduces germination rate of leafy spurge seed, we believe most of the increase in 1994 consisted of a flush of seedlings, which subsequently died due to competition with established plants(Hanson and Rudd 1933, Selleck et al. 1962).

No control of leafy spurge relative to pretreatment stem density was evident with any treatment in the first year after beetles were released, and the unanticipated need to reburn the most successful colonies prevented meaningful assessment of control during the second year. Given the small founding populations used in this study, lack of control during the first year was not unexpected.

However, results from leafy spurge-infested fields at Northern Prairie Wildlife Research Center indicate that prerelease burning can have immediate control benefits when larger numbers of beetles are released. As part of an operational control program (Fellows, Unpublished data), releases of approximately 1,000 *A. nigriscutis* were made in July 1996, at intervals of about 25 m throughout a habitat unit where the species was known to do well. Approximately half of the unit had been burned in early June 1996. The remainder had not been burned since at least 1967. In late May 1997, we estimated

Table 4. Change in mean number of leafy spurge stems m^{-2} (SE) by treatment and year. Values are least-squares means.

Treatment	All Plots n	All Plots 1993 to 94	All Plots 1993 to 95	Beetles Present 1995 & 1996 n	Beetles Present 1995 & 1996 1993 to 94	Beetles Present 1995 & 1996 1993 to 95
		(Δ stems m^{-2})	(Δ stems m^{-2})		(Δ stems m^{-2})	(Δ stems m^{-2})
Control	9	11.9 (24.1)a	18.9 (23.3)a	7	13.8 (24.6)a	24.8 (21.4)a
Unburned	26	21.6 (13.9)a	5.7 (13.8)a	7	31.7 (24.6)a	-20.2 (21.4)a
Fall preburn	9	135.4 (24.1)b	37.0 (23.3)a	5	141.7 (29.1)b	31.3 (25.3)a
Spring preburn	9	110.1 (24.1)b	24.5 (23.3)a	5	124.8 (29.1)b	33.7 (25.3)a

$^{a-b}$ Means within a column with different superscripts are different ($p<0.05$).

the size of the spurge-free zone at each release site. For 25 sites in the burned habitat, the mean spurge-free radius (SE) was 93 (12) cm, compared to a mean of 36 (9) cm at 10 unburned sites. Mean values at reference sites midway between adjacent release sites were 11 (1) cm in the burned and 15 (1) cm in the unburned zone.Thus beetles on average cleared nearly 7 times more spurge in the burned (2.7 m^2) than in the unburned (0.4 m^2) habitat during the first year. Additionally, zones of reduced stem density and stunting extended for 3–4 m around most of the sites in the burned, but not in the unburned area.

Because economics and long-term control benefits of preburning fields solely to enhance establishment of *A. nigriscutis* have not been determined, we cannot currently recommend that prerelease burning be adopted as an operational practice. However, managers should take advantage of scheduled management burns in leafy spurge-infested fields by releasing *A. nigriscutis* into suitable habitat within the burned area whenever possible.

Our results also demonstrate that established *A. nigriscutis* colonies in North Dakota can survive burns from early October through mid-May. No difference was found in the population indexes of burned and unburned plots, suggesting that burning had no negative effect on larval survival and eclosure rates. Moreover, based on the response of beetles to preburned release sites, we anticipate that periodic burning at appropriate times will enhance expansion of established colonies and lead to earlier control of leafy spurge.

Spring burning of established colonies must be completed early enough to allow spurge to regrow before beetles emerge. Based on regeneration observed in this study, adequate spurge would probably be available in southeastern North Dakota following burns as late as 25 May in most years. However, assuming regeneration is moisture dependent, a target cutoff date of 15 May is recommended during dry years. Elsewhere, the spring cutoff should be adjusted to match the anticipated local adult emergence pattern and rates of foliar regeneration.

Because egg laying is complete by early September (Rees and Spencer 1991), fields containing *A. nigriscutis* can likely be burned as early as 1 September without damage to colonies. Even earlier burning, if needed to meet grassland management objectives, may have no negative effect. Brinkman (1997) found peak insemination rates in early July and few adults by early August at an *A. nigriscutis* insectary near Pollock, South Dakota. Burning as early as 1 August may therefore not substantially reduce egg production. However, because mid-summer burning could affect the nutrient value of spurge or increase soil insolation beyond larval tolerance, early burning should be approached with caution.

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J. Range Manage.
52:494–499 September 1999

Leaf area, visual obstruction, and standing crop relationships on Sandhills rangeland

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Abstract

The objective of this study was to determine if leaf area index (LAI) or visual obstruction (VO) could be used in an efficient double-sampling format for estimating total above-ground standing crop on upland range sites in the Nebraska Sandhills. Sampling was conducted in pastures used for summer grazing research in which treatments consisting of stocking at 16, 32, or 48 animal-unit-days (AUD) ha^{-1} in June or July and an ungrazed control that were replicated 3 times. During trial 1, LAI, VO, and yield of standing crop were measured in 1995 and 1996 at 12 random sampling sites in each of twenty-one, 1.0-ha pastures. Trial 2 compared modified LAI and VO sampling procedures against those used in trial 1. Modifications included the use of a circular 0.25 m^2 sample plot area rather than a rectangular one and increasing both the number of LAI and visual obstruction readings that were used in the calculation of the mean value at each sampling site. During trial 2, data were collected from 12 sampling sites within each of 14 pastures that comprised 2 blocks of grazing treatments. There was a significant ($P<0.01$) linear relationship between LAI and yield of standing crop during trial 1, but only 33% of the variation in standing crop was attributable to LAI. The modified LAI sampling procedure increased R^2 to 0.59. Similarly, the relationship between visual obstruction and standing crop was significant ($P<0.01$), but R^2 values were only 0.31 and 0.41 during the first and second years of trial 1, respectively. The modified visual obstruction (VO) sampling procedure resulted in only minimal R^2 improvement compared to the trial 1 method. Pooling LAI or VO data for individual sample sites into stocking rate means resulted in the detection of significant ($P<0.01$) quadratic relationships between fall LAI or VO and summer stocking rate. Based on the sampling procedures used in this study, neither LAI nor VO would be useful as direct predictors of total standing crop at individual sample locations on upland range sites in the Nebraska Sandhills. However, with pastures as experimental units, these methods can detect the relative effects of stocking rate with replicated treatments.

Key Words: total above-ground biomass, double-sampling, LAI, plant canopy analysis

Resumen

El objetivo de este estudio fue determinar si el índice de área foliar (IAF) o la obstrucción visual (OV) pudieran ser utilizados en un formato eficiente de doble-muestreo para estimar la cosecha en pie aérea total de los sitios de pastizal altos de Nebraska Sandhills. El muestreo se condujo en potreros utilizados para investigación de apacentamiento en verano, en la que los tratamientos fueron cargas animal de 16, 32 o 48 unidades-animal-día ha^{-1} en Junio o Julio y un control sin apacentamiento, los tratamientos tuvieron 3 repeticiones. Durante el ensayo 1, el IAF, la OV y el rendimiento de la cosecha en pie se midieron en 1995 y 1996 en 12 sitios de muestreo elegidos aleatoriamente en cada uno de los 21 potreros de 1 ha. En el ensayo 2 se compararon los métodos de muestreo modificados para el IAF y OV contra los utilizados en el ensayo 1. Las modificaciones incluyeron el uso de una parcela de muestreo circular de 0.25 m^2 en lugar de una rectangular e incrementando el número de lecturas tanto para el IAF como para la OV y que fueron utilizadas para calcular el valor de la media de cada sitio de muestreo. En el ensayo 2, los datos se colectaron en 12 sitios de muestreo dentro de cada uno de los 14 potreros que comprendían 2 bloques de tratamientos de apacentamiento. En el ensayo 1 hubo una relación lineal significativa ($P<0.01$) entre el IAF y la cosecha en pie, pero solo el 33% de la variación de la cosecha en pie fue atribuible al IAF. El muestreo modificado de IAF incremento el R^2 a 59%. De igual manera, la relación entre la OV y cosecha en pie fue significativa ($P<0.0$ 1), pero los valores de R^2 fueron solo del 0.31 y 0.41 durante el primer y segundo años del ensayo 1 respectivamente. El procedimiento modificado de muestreo de OV resulto en un mejoramiento mínimo de los valores de R^2 comparado con el método del ensayo 1. La combinación de los datos de IAF y OV para cada sitio individual de muestreo con las medias de carga animal resulto en la detección de una relación cuadrática significativa ($P<0.01$) entre el IAF y la OV de otoño y la carga animal de verano. Basado en los procedimientos de muestreo utilizados en este estudio, ni el IAF ni la OV son útiles para predecir directamente la cosecha en pie total a nivel de localidad individual de muestreo de los sitios de pastizal elevados de Nebraska Sandhills. Sin embargo, con los potreros como unidades experimentales y con tratamientos repetidos, estos métodos pueden detectar los efectos relativos de la carga animal.

Published with the approval of the director of the Univ. of Nebraska-Lincoln, Institute of Agric. and Natur. Resources, Ag. Res. Div. as Journal Ser. no. 12296

The authors thank Troy M. Walz, Alexander J. Smart, and Gordon D. Moeller of the University of Nebraska-Lincoln and Virginia Emly, Tom Landel, and Cindy Schippenwright of the USDA-Forest Service for technical assistance.

Manuscript accepted 19 Oct. 1998.

Standing crop or above-ground herbage biomass is an important quantitative variable needed in grazing studies and in the characterization of plant communities. Estimation of standing crop has traditionally been accomplished by hand-clipping, drying, and weighing vegetation from plots of known area. This technique is slow, labor intensive, and destructive. Several methods utilizing remote sensing for non-destructive standing crop estimation were reviewed by Tucker (1980). Others have used double-sampling procedures where hand-clipping was combined with visual weight estimation (Pechanec and Pickford 1937), disk meters (Sharrow 1984), or electronic capacitance meters (Neal and Neal 1981). Success has ranged from poor to excellent. Plant growth stage and plant community type were 2 important factors associated with the accuracy and precision of some of these approaches.

Non-destructive vegetation analysis can be accomplished with a plant canopy analyzer (Welles and Norman 1991) which provides rapid estimations of leaf area index (LAI) and quantifies other characteristics of canopy architecture. This technology has been used to quantify architecture of field crops and to characterize forage utilization intensity on rangeland (Miller-Goodman et al. 1999). Another non-destructive method of measuring vegetation involves visual obstruction. In studies in northeastern Kansas, Robel et al. (1970) found a significant correlation between visual obstruction (VO) and total standing crop. Obstruction measurements were taken by visually sighting towards a round pole that had alternating decimeters painted brown and white. The lowest decimeter mark visible on the pole was recorded as the obstruction measurement. Visual obstruction data are collected and used by several state and federal land management agencies for the purpose of monitoring grazing practices and the status of wildlife habitat; particularly for upland game birds, where density and height of vegetation are important factors (Price 1987, PGTC 1995). The objectives of this study were to quantify the relationship of LAI and VO to standing crop, the relationship of LAI to VO, and the effects of summer stocking rate and grazing pressure on fall LAI and VO on upland range sites in the Nebraska Sandhills. Correspondingly, the potential of using LAI or VO methods in a double-sampling technique to estimate standing crop was evaluated.

Materials and Methods

The study was conducted at the University of Nebraska, Gudmundsen Sandhills Laboratory, 11 km northeast of Whitman, Neb. Soils of the study pastures are Valentine fine sands (mixed mesic Typic Ustipsamment) derived from an eolian sand parent material. Vegetation is dominated by mid and tall grasses including little bluestem, [*Schizachyrium scoparium* (Michx.) Nash], sand bluestem (*Andropogon hallii* Hack.), and prairie sandreed [*Calamovilfia longifolia* (Hook.) Scribn.]. Other common species are hairy grama (*Bouteloua hirsuta* Lag.), sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], prairie junegrass [*Koeleria macrantha* (Ledeb.) Schult.], switchgrass (*Panicum virgatum* L.), western ragweed (*Ambrosia psilostachya* DC.), and sedges (*Carex* spp.).

Leaf area index (LAI), visual obstruction (VO), and standing crop sampling was conducted in twenty-one, 1-ha pastures in which 7 grazing treatments were replicated 3 times. Treatments were stocking rates of 16, 32, and 48 animal-unit-days (AUD) ha^{-1} in either June or July and an ungrazed control. Treatments resulted in a range of mean standing crop values of 880 to 2,810 kg ha^{-1} in October.

Leaf area index measurements were taken using a LICOR LAI-2000 plant canopy analyzer[1]. Operational theory of this instrument is based on radiation interception and measurements of how quickly radiation is attenuated as it passes through a vegetation canopy (LI-COR Inc. 1991). The probability of radiation interception is related to foliage orientation and is proportional to path length and foliage density (Welles and Norman 1991). A complete sampling sequence first requires a measurement of sky brightness with the sensor held above the canopy followed by 1 or more readings taken below the canopy. The sensor utilizes fisheye optics to project a hemispheric image of the canopy onto 5 silicon detectors that are arranged in concentric rings. A microcomputer processes the data and calculates leaf area index (LAI), leaf mean tilt angle (foliage orientation), and standard errors. Attenuation of diffuse sky radiation is measured simultaneously at 5 zenith angles (7°, 23°, 38°, 53°, and 68°). The ratio of each ring's signals (below to above) is then assumed to be equivalent to the canopy's gap fraction at that ring's viewing angle. By measuring attenuation at several angles from the zenith, foliage orientation information also can be obtained (Welles and Norman 1991).

An important consideration for the sensing optics is some restriction to mask out the operator or the sun. For this study, an opaque cover that restricted the viewing area to 45° was placed on the sensor. Welles and Norman (1991) and Miller-Goodman et al. (1999) also recommended this narrower field of view to correctly integrate gaps and canopy structure that are characteristic of heterogeneous vegetation with large gaps. Our sampling took place on days that ranged from mostly sunny to cloudy. Under sunny conditions, the area surrounding the sensor was shaded with an umbrella because sunlit leaves detected by the sensor would have underestimated LAI.

Equipment used for visual obstruction (VO) measurement was similar in design to that used by Robel et al. (1970). Our equipment consisted of 2 poles (3 cm diameter X 120 cm length) that were connected by a nylon cord fastened at a height of 1 m on each pole. Length of the cord was 4 m. The reading pole was painted in 36 alternating bands (2.54 cm wide) of gray and white. The bands were numbered in ascending order beginning with 1 at the bottom. The procedure for visual obstruction measurement consisted of 1 person holding the reading pole vertically in the center of a 0.25 m^2 quadrat area. A second person, the observer, would place the other pole at a distance of 4 m. Looking from a height of 1 m, the observer would read the number of the lowest band not obstructed by vegetation.

Trial 1

Trial 1 was conducted in October 1995 and 1996. Within each of the 21 pastures, 3 stratified transects were

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[1] LI-COR Incorporated, 4421 Superior Street, Lincoln, Neb 68504.

Mention of a trade name or product does not constitute a recommendation or endorsement for use by the University of Nebraska.

established with each transect having 4 randomly selected sampling sites (252 total per year). At each sample site, LAI and VO measurements were taken followed by the centering of a 25 × 100 cm quadrat frame (0.25 m^2) over the sampling point and hand-clipping all vegetation, current- and preceding-year's herbage, to a height of 2 cm. The canopy analyzer measures light attenuation above the 2 cm height. Harvested material was oven-dried at 60°C to a constant weight.

The procedure for leaf area index (LAI) measurements consisted of programming the instrument for an above-canopy calibration reading followed by 3 below-canopy readings (3 LAI measurements). Below-canopy readings were with the sensor on the soil surface at 3 locations (33, 67, and 100 cm) along the 100-cm length of the rectangular quadrat area. The mean of the 3 LAI measurements was considered the LAI for the sample site.

Visual obstruction (VO) readings were made from opposite sides of each sample site perpendicular to the predominant slope. If topography prevented both measurements from being taken in the same vertical plane, the observer would take the second reading in the same horizontal plane from a position less than 180° from the first reading point. The mean of the 2 visual obstruction readings was considered the VO for the sample site.

Trial 2

Trial 2 was conducted in March 1997. Based on the results of trial 1, sampling procedures for LAI and VO measurements were modified and compared with procedures used in trial 1 to determine if improvement could be made in the relationship between leaf area index (LAI) and standing crop or visual observation (VO) and standing crop. The modifications included using a circular 0.25 m^2 plot frame rather than a rectangular quadrat and increasing both the numbers of LAI and VO readings that were used to calculate mean values for each sample site.

For trial 2, 12 sampling sites for LAI, VO, and standing crop measurements were selected in each of 14 pastures (168 total). Methods for LAI estimation included (1) 1 above-canopy and 3 below-canopy readings (as in trial 1) and (2) 1 above-canopy and 8 below-canopy readings. For LAI method 1, the 3 below-canopy readings were taken in a straight line through the center of the circular plot area. For the modified LAI method 2, the 8 below-canopy readings were taken with the sensor placed at an equally-spaced distance around the perimeter of the circular plot area. With this method, the unobstructed view of the LAI sensor was always towards the center of the plot.

Methods for determining VO included (1) 2 readings, as in trial 1, and (2) 4 readings, 1 from each cardinal direction. For both LAI and VO methods, the mean of the multiple readings was used as the LAI or VO value for that sample site. After LAI and VO measurements were taken, vegetation in the plot area was hand-clipped to a height of 2 cm and oven-dried at 60°C to a constant weight.

Regression analysis (SAS Institute Inc. 1985) was used to evaluate the relationships of LAI and VO to standing crop, with standing crop as the dependent variable. Visual obstruction data were multiplied by 2.54 to convert readings to cm. Regression analyses were also used to evaluate the relationship between LAI and VO, and the effects of summer stocking rate (AUD ha^{-1}) on fall LAI and VO. The level of probability selected for significance was $P \leq 0.05$.

Results and Discussion

Leaf Area Index

Collecting leaf area index (LAI) data using the canopy analyzer was relatively rapid averaging less than 2 minutes per sample site when taking 3 below-canopy readings. This included walking time in the 1-ha pastures. Mean LAI recorded during sampling in 1995 and 1996 (trial 1) was 0.97, and ranged from 0.08 to 3.12. Mean yield of standing crop during the 2 years was 148.4 g m^{-2} with a range of 15.2 to 656 g m^{-2}. A significant ($P<0.01$) linear relationship occurred between standing crop and LAI during 1995 and 1996. Year did not affect the relationship between LAI and standing crop ($P>0.05$), therefore, data were pooled across the 2 years. The relationship was poor with only 33% of the variation in standing crop being attributable to LAI (Fig. 1).

The mean LAI recorded during trial 2 was 0.83 (range 0.07 to 2.84) using the 3-reading method and 0.80 (range 0.05 to 3.40) using the 8-reading method. Mean standing crop for trial 2 was 125.2 g m^{-2} with a range of 15.6 to 437.2 g m^{-2}. For the 3-reading method, LAI accounted for 16% more of the variation in standing crop in trial 1 than in trial 2 (Fig. 1 and 2a). The 8-reading method resulted in the strongest relationship between LAI and standing crop (R^2 = 0.59) and was most effective in reducing residual differences when LAI was greater than 1.0 (Fig. 2b).

A significant ($P<0.01$) quadratic relationship between fall LAI and summer stocking rate (0, 16, 32, and 48 AUD ha^{-1}) occurred when LAI data for sample sites pooled within stocking rates (Fig. 3). Year had a significant effect ($P<0.01$), and R^2 values were 0.94 in 1995 and 0.71 in 1996. Higher rates of herbage

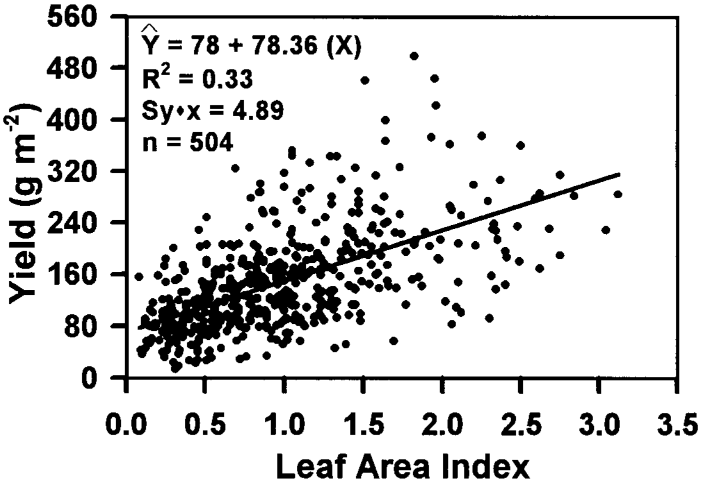

Fig. 1. Relationship between leaf area index (LAI) and standing crop yield in trial 1 during 1995 and 1996. Sy u x is the standard error of the estimate.

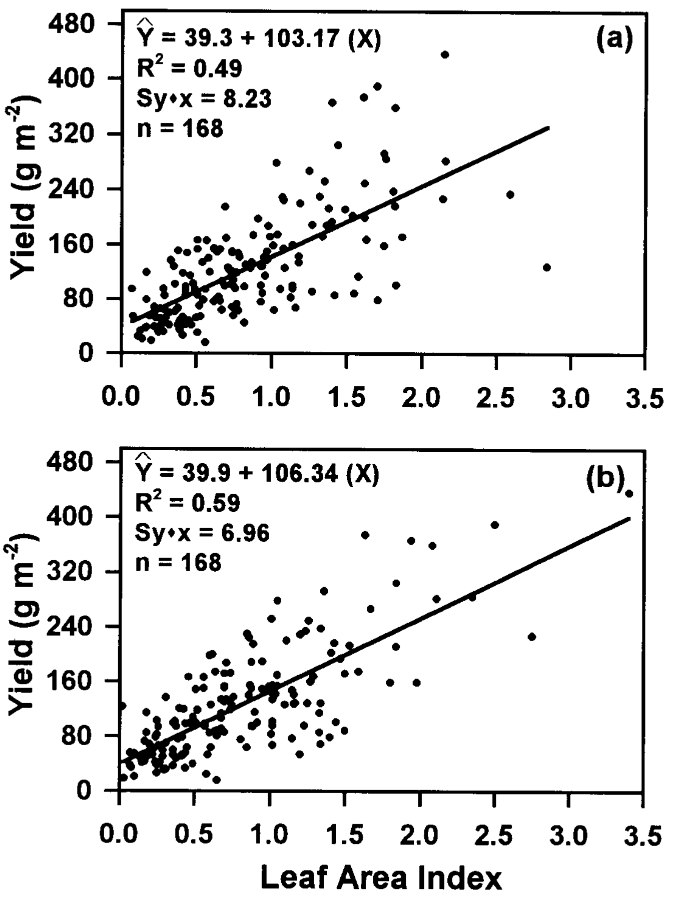

Fig. 2. Relationship between leaf area index (LAI) and standing crop yield (a) using the mean of 3 readings per sample and (b) using the mean of 8 readings per sample in trial 2, 1997. Sy u x is the standard error of the estimate.

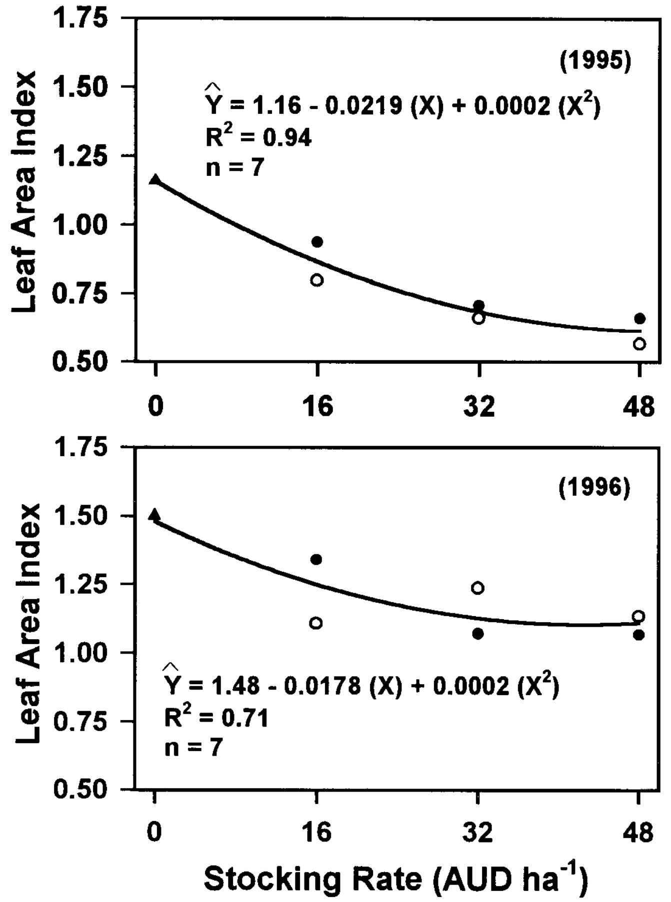

Fig. 3. Effects of stocking rate in June (○) or July (●) on fall leaf area index (LAI) during 1995 and 1996.

production from mid-June to mid-July in 1996 than in 1995 (Cullan 1997), may have caused larger differences between months after light (16 AUD ha^{-1}) and moderate (32 AUD ha^{-1}) stocking rates in respective years. An additional month for plant growth after June grazing (June to October vs. July to October) also contributed variation. Miller-Goodman et al. (1999) reported significant linear relationships (R^2 = 0.95 to 0.99) between change in LAI (pre- and post-grazing) and stocking rate.

Visual Obstruction

The mean visual obstruction (VO) recorded during 1995 and 1996 (trial 1) was 3.6, and the range was from 1.0 to 11.5. There was a significant ($P<0.01$) linear relationship between VO and standing crop with an 82% greater rate of change in VO per unit change in yield in 1996 than in 1995 (Fig. 4). The relationship was relatively poor with an R^2 value of 0.31 in 1995 and 0.41 in 1996.

During trial 2, mean VO recorded was 2.9 (range 1.0 to 7.5) using the 2-reading method and 3.0 (range 1.0 to 7.3) using the 4-reading method. As in trial 1, a relatively poor linear relationship was observed between VO and standing crop for both methods (Fig. 5). Increasing the number of readings to 4 per sample site accounted for only 8% more of the variance in standing crop than when making 2 readings per site.

Robel et al. (1970) reported an R^2 value of 0.96 when 10 observations per transect were pooled and used to predict standing crop. In contrast, we found pooling observations from 12 sample sites into pasture means did not improve the strength of the relationship between VO and standing crop. Pooling VO data for individual sample sites into stocking rate means resulted in the detection of a significant ($P<0.01$) quadratic relationship between fall VO and summer stocking rate (Fig. 6). Year had a significant effect ($P<0.01$), and R^2 values were 0.89 in 1995 and 0.88 in 1996. A similar type of relationship was observed between fall LAI and summer stocking rate (Fig. 3) because of a strong correlation between LAI and VO (r = 0.93 in 1995 and r = 0.71 in 1996). Vegetation type, structure, and density are likely to have a significant affect on VO. The work by Robel et al. (1970) was conducted on several Flint Hills range sites with an average standing crop of about 232 g m^{-2}, 57% more standing crop than during trial 1 and 88% more standing crop than in trial 2 of our study. Vegetation in our study pastures was heterogeneous in terms of basal cover and species composition including short-, mid-, and tall-statured grasses. Robust plants, outside the sampling area clipped for yield, were occasionally located in the line of sight, obstructing the reading pole and providing an over-estimate of VO for herbage harvested inside the sampling area.

Variability in plant type, height, and distribution also can cause a similar type of error when sampling leaf area index (LAI). With minimal canopy cover within the quadrat area, the canopy analyzer optics will sense beyond the boundary of a 0.25 m^2 quadrat. If there was substantial canopy cover in the periphery area, the result would be an over-estimation of LAI for the quadrat area. Increasing quadrat size may have reduced this problem. When hand-clipping for standing crop estimation on the same range type, Brummer et al. (1994) reported that variance was reduced and efficiency improved when quadrat size was increased.

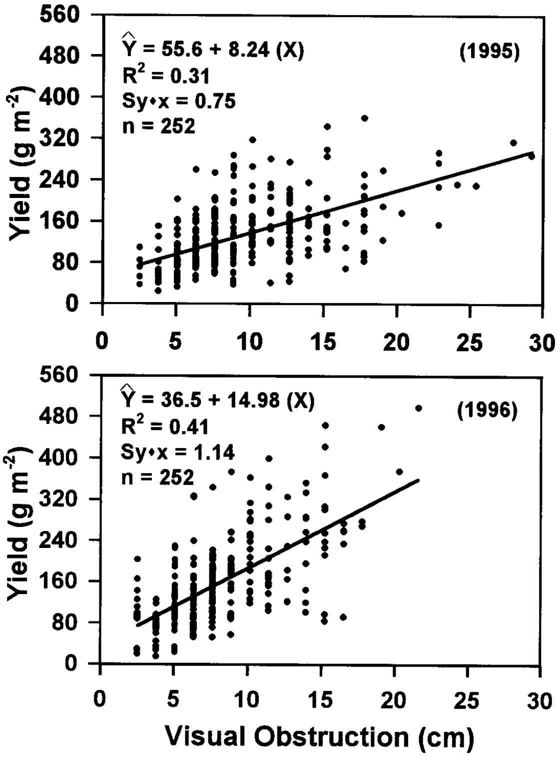

Fig. 4. Relationship between visual obstruction and standing crop yield in trial 1 during 1995 and 1996. Syu x is the standard error of the estimate.

Conclusions

Based on the sampling procedures described, visual obstruction measurements would probably not be useful in a double-sampling technique for prediction of total above-ground herbage standing crop on upland range sites in

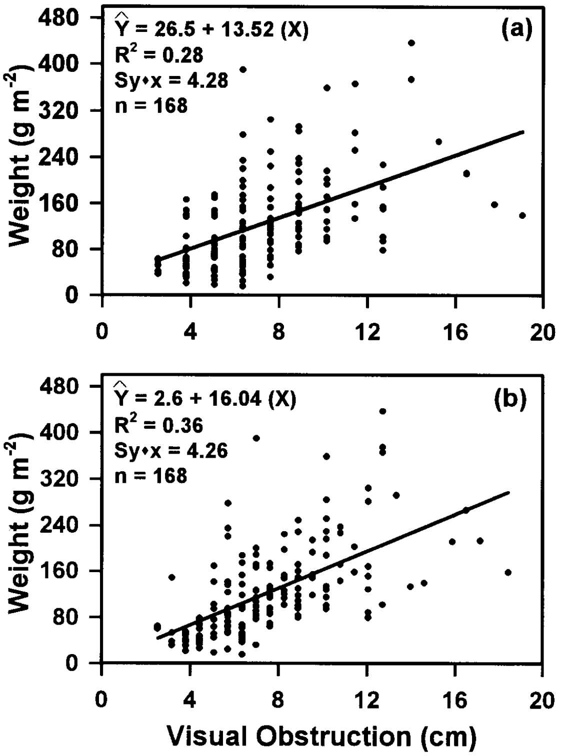

Fig. 5. Relationship between visual obstruction and standing crop yield (a) using the mean of 2 readings per sample and (b) using the mean of 4 readings per sample in trial 2, 1997. Syu x is the standard error of the estimate.

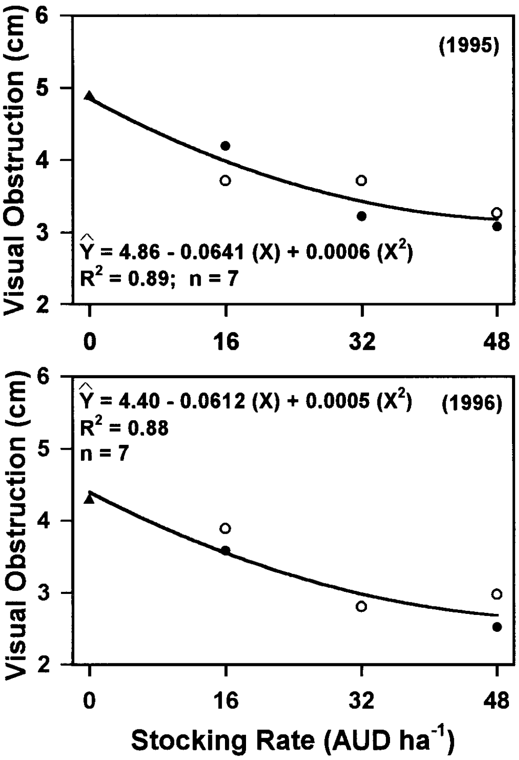

Fig. 6. Effects of stocking rate in June (○) or July (●) on fall visual obstruction during 1995 and 1996. Syu x is the standard error of the estimate.

the Nebraska Sandhills. Leaf area index and standing crop relationships were generally stronger. Our most successful approach, using 8 below-canopy leaf area index (LAI) readings for a circular 0.25 m^2 plot area, resulted in an R^2 value of 0.59 and a standard error of the estimate of 6.96. However, the strength of this relationship could probably be matched or surpassed using a double-sampling procedure with visual estimates and hand-clipping to estimate yield with lower equipment costs. One disadvantage associated with LAI, visual obstruction (VO), and other indirect sampling methods, is that only the total vegetation weight is estimated. In many situations, it is necessary to distinguish between current- and previous-year's herbage especially when calculating grazing pressure. Additionally, estimates of yield may be needed for individual species or groups.

With replicated pastures, however, canopy analyzer and VO methods can be used to efficiently detect the relative effects of stocking rate treatments. The practical value and/or meaning of this information is important when considering vegetation canopy characteristics and grazing variables, and their association with micro-climate, snow catch, insect populations, or wildlife habitat.

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52:500–507 September 1999

Assessing grazing impacts by remote sensing in hyper-arid environments

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Abstract

Assessing vegetation status via remote sensing techniques using various vegetation indices has been successfully applied to semi-arid and arid environments. We tested the feasibility of applying such techniques for assessing grazing impact in hyper-arid environments with a high variance in soil type over space. An anticlinal erosional cirque called Makhtesh Ramon in the Negev desert, Israel, was selected for the study. The cirque is typified by low rainfall (40–90 mm per year), a variety of soil substrates and is subject to grazing by a herd of Asiatic wild asses (*Equus hemionus*) reintroduced into the cirque between 1984 and 1987. As a control, we used an ungrazed dry riverbed south of the cirque that runs parallel to the riverbed draining the cirque. We used 5 common vegetation indices derived from Landsat 5 satellite Thematic Mapper (TM). Four images were used, representing dry and wet seasons in above- and below-average rainfall years (1995 and 1987, respectively). To test whether we can detect changes in plant community structure via satellite data we correlated vegetation indices from the TM to ground measurements made along the altitudinal gradient of the cirque. To test whether differences in plant cover could be detected, we correlated the vegetation indices with ground measurements of cover in and out of the cirque (grazed and ungrazed areas). Although ground measurements showed that community structure changed following grazing with altitudinal gradient and ground cover was 30% lower inside the cirque than outside the cirque, none of the 5 vegetation indices correlated with the ground measurements. Transformed Soil Adjusted Vegetation Index (TSAVI) and Normalized Difference Vegetation Index (NDVI) produced the best results. We hypothesize that the low vegetation cover that typifies hyper-arid environments increases the noise to signal ratio. Thus, a 30% decline in vegetation cover in this case is only an absolute decline of 4% from 15.8 to 11.2%. Because TM is sensitive to absolute cover rather than the relative differences, it is difficult to demonstrate differences among TM images. Using ANOVA to test the effect of season and grazing status on TSAVI and NDVI, we found a significant interaction between season and grazing status in 1995 with indices declining more from wet to dry season inside the cirque than outside the cirque. No such pattern was found in 1987. These data suggest that satellite imagery may detect changes in plant cover over time but can not serve as a direct index of plant cover in hyper-arid conditions.

Key Words: Asiatic wild ass, reintroduction, satellite, vegetation cover

Resumen

Se estimó el estado de la vegetación via técnicas de teledetección usando varios índices de vegetación que han sido satisfactoriamente aplicados a semi-áridos y áridos ambientes. Se ensayó la factibilidad de aplicar estas técnicas para estimar el impacto de la herbivoría en ambientes hiper-áridos con gran varianza del tipo de suelo en el terreno. El "Makhtesh Ramon", un anticlinal erosional círculo en el desierto del Negev, Israel, fue seleccionado para el estudio. El círculo es caracterizado por una baja precipitación (40-90 mm por año) y una variedad de sustratos edáficos, además es expuesto a forrajeo por un rebaño de asnos salvajes asiáticos (*Equus hemionus*) reintroducidos en el círculo entre 1984 y 1987. Como control, se uso un no forrajeado lecho seco de un rio al sur del círculo el cual corre paralelo a el lecho del rio drenando el círculo. Se usaron 5 índices de vegetación derivados del satélite Landsat 5 Thematic Mapper (TM). Cuatro imagenes fueron usadas, representando estaciones secas y humedas en años con altos-y bajos- promedios de precipitación (1995 y 1987, respectivamente). Para probar si es posible detectar cambios en la estructura de la comunidad vegetal utilizando datos de satélite se corrrelacionaron los índices de vegetación del TM con mediciones de la vegetación hechas a lo largo de un gradiente altitudinal en el círculo. Para probar si las diferencias en covertura de la vegetación podrian ser detectadas, se correlacionaron los índices de vegetación con las medidas de covertura del suelo dentro y fuera del círculo (forrajeadas y no forrajeadas áreas). Aunque las mediciones

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This study was funded by the International Arid Lands Consortium, The Fund for Threatened Wildlife of the Frankfurt Zoological Society, the Israel Nature Reserves Authority, and the Israel Ministry of Science. This is publication No. 279 of Mitrani Department of Desert Ecology and publication No. 75 of the Ramon Science Center.

Manuscript accepted 6 Dec. 1998.

de la vegetación muestran que la estructura de la comunidad cambia seguidamente del forrajeo cuando el gradiente altitudinal y la covertura del suelo fue 30% menor dentro del círculo que fuera del círculo, ninguna de los 5 índices de vegetación estan correlacionados con las medidas de la vegetación."Transformed Soil Adjusted Index" (TSAVI) y "Normalized Difference Vegetation Index" (NDVI) produjeron el mejor resultado. Nuestra hipótesis es que la baja covertura de la vegetación que tipifica los ambientes hyper-áridos incrementa la razón entre "el ruido y la señal". De este modo, un decrecimiento del 30% en la covertura de la vegetación en este caso es sólo un decrecimiento absoluto del 4% del 15.8 al 11.2%. Debido a que el TM es sensitivo a la covertura absoluta antes que a las diferencias relativas, es dificil demostrar las diferencias entre imagenes del TM. Usando ANOVA para probar el efecto de las estaciones y el estado de forrajeo en TSAVI y NDVI, se encontró una interacción significante entre estaciones y estado de forrajeo en 1995 con los índices declinando más desde la estación humeda a la seca dentro del círculo que fuera del círculo. Este patrÛn no fue encontrado en 1987. Estos datos sugieren que las imagenes de satélite pueden detectar cambios sobre el tiempo pero no pueden servir como un directo índice de la covertura de la vegetación en condiciones hiper-áridas.

Remote sensing techniques have long been applied for the quantitative and qualitative evaluation of vegetation in semiarid ecosystems. Many studies have demonstrated their utility in assessing vegetation distribution (Colwell 1974, Justice et al. 1985, Sellers 1985, Tucker 1979) and their potential to overcome the manpower and fiscal restrictions that limit large-scale ecological surveys (Pickup et al. 1994). Visible and near-infrared (NIR) multispectral images are the most useful data to examine vegetation patterns and corresponding ecological processes at regional and global scales. Vegetation indices (VI) (Elvidge and Chen 1995) derived from remotely sensed data have frequently been proposed as a method for predicting green biomass. In remote sensing applications VIs play a significant role for qualitatively and quantitatively evaluating vegetation cover by contrasting intense chlorophyll pigment absorption in the red against the high reflectivity of plant materials in the NIR (Tucker 1979). Specifically, indices of variables such as percent green cover, leaf area index (LAI) or absorbed photosynthetically active radiation (APAR) are sought (Anderson et al. 1993, Bannari et al. 1995, and Chilar et al. 1991).

More than any other regions, arid lands are susceptible to land degradation due to overgrazing and other human related activities. Because of the large-scale surveys required to assess such degradation, standard methodologies are often economically and logistically prohibitive, making remote sensing an attractive alternative (Pickup and Chewing 1994). However, vegetation sparseness in these regions means that soil is a dominant factor in remotely-sensed measurements, making measurement of plant cover complicated by the variability in the soil reflectance, as well as spectral interactions between the sparse plant canopies and the soil background.

Considerable effort in remote sensing has been focused on the optimization of soil-adjusted vegetation indices (Elvidge and Chen 1995, Huete 1986, 1988) and their successful application to semiarid regions (Foran 1987, Franklin 1991, Graetz et al. 1988, Pech et al. 1986, Williamson 1989). Studies on the use of remote sensing for assessing the impact of livestock grazing on vegetation cover and land degradation in arid and semi-arid areas are numerous (Graetz and Gentle 1982, Bastin et al. 1993a, 1993b, Pickup et al. 1993, Pickup and Chewing 1994, Pickup 1995). However, no attempts have been made to use these techniques in hyper-arid environments. Hyper-arid environments are especialy problematic in this respect because of high spatial variance in soil types and high variance in vegetation cover over both space and time. In this study we apply and evaluate well-used VIs from satellite data for detecting grazing impacts in a hyper-arid environment, and compare it with ground measurements of vegetation.

Methods

Study Area

The study area was Makhtesh Ramon - an anticlinal 200 km^2 erosional cirque in the southern boundary of the Negev highlands (30° 35’ N, 34° 45’ E), Israel (Fig. 1). The cique is elongated, running SW-NE with the floor tilted downwards towards the northeast. The Ramon dry riverbed, running NE down the center of the cirque exiting through a break in the southern rim, drains it. The north rim of the cirque consists of a sheer 200 m drop from the Negev highlands. Rim altitude ranges between 800 and 900 m, while the cirque floor ranges from ca. 800 m at the SW edge to ca. 400 m in the NE basin. The southern rim is less steep, and is a ridge with a crest at about 510 m. A dry riverbed, Nahal Nekorot, runs parallel to the Ramon riverbed along the southern foothills of the southern rim. The altitudinal gradient from west to east along the Ramon and Nekorot riverbeds is correlated with rainfall, which ranges from about 95 mm in the southwest to about 40 mm in the northeast (Ward et al. 1993).

We selected Makhtesh Ramon for 3 reasons:

(1) A wide range of soil types and highly variable precipitation patterns typify the region. Exposed substrates include sandstone, gypsum, limestone, dolomite and various clays and several basalt hills (Danin 1983). The strong environmental changes (rainfall, and temperature) are reflected in the vegetation. The area is a transition from the steppe vegetation in the north to the true desert vegetation in the south (Ward and Olsvig-Whittaker 1993, Ward et al. 1993). The vegetation consists mostly of perennials. The cover and the diversity of the vegetation are higher in the wadis than on the rim and on the hills. For further details of the substrates and vegetation communities in Makhtesh Ramon, see Ward et al. (1993).

(2) Human pressure in Makhtesh Ramon and neighboring areas has increased considerably over the past decade, including tourism by off road vehicles and increased military activity that may induce land degradation and erosion.

(3) The successful reintroduction of an Asiatic wild ass (*Equus hemionus*) population into this region and its projected rapid growth rate may lead to eventual overgrazing. The reintroduction began in 1982 and included 4 releases totaling 28 animals (14 males and 14 females). The population has adapted well to the wild and grew rapidly. In 1996 the population was estimated at 100 animals and is expected to double by 2006 (Saltz and Rubenstein 1995).

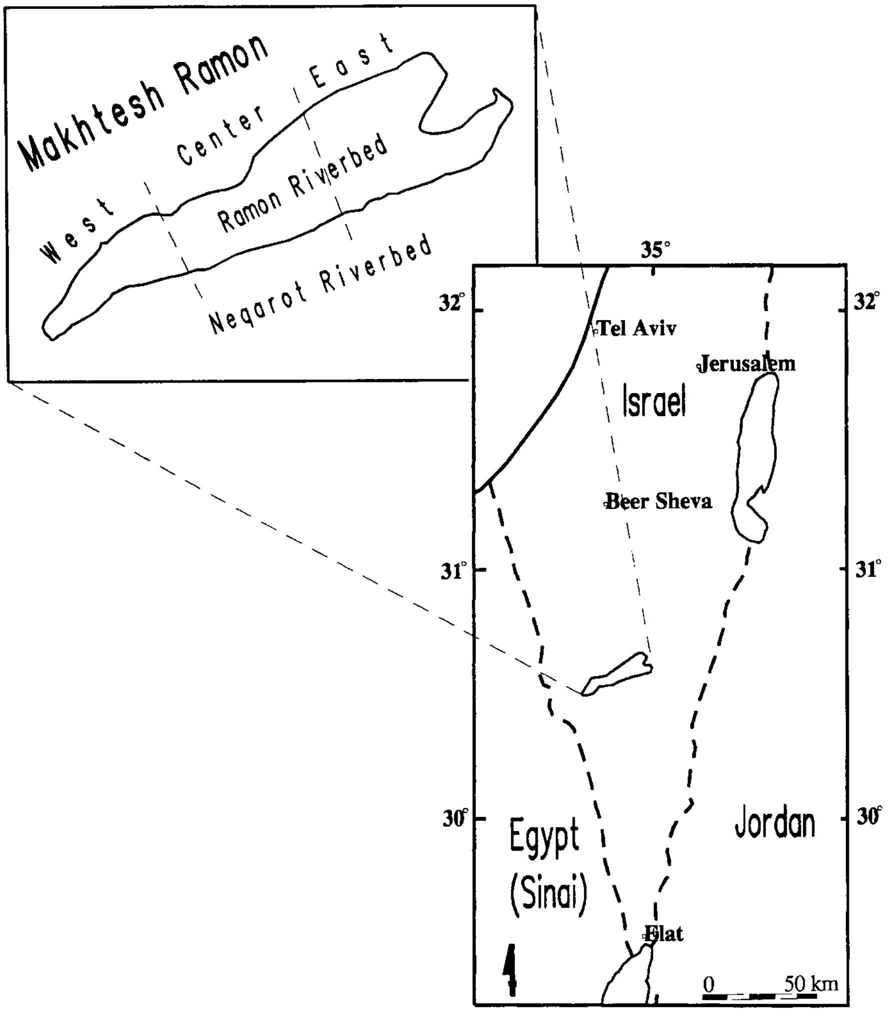

Fig. 1. The study areas in Israel.

Satellite Data Processing

We used 4 Landsat 5 Thematic Mapper (TM) images of the study region with a spatial resolution of 30 m. The satellite images represent the end of rainy (March–April) and dry season (August–September) of the years 1987 and 1995. Winter 1986/87 was dry with less than average rainfall, while winter 1994/95 had an above average rainfall. Therefore, the Landsat TM images from 1987 and 1995 represent “wet” and “dry” years, respectively.

The pre-processing of the Landsat TM data in this study includes several correction algorithms carried out in several steps, including radiometric, atmospheric, and geometric corrections of the Landsat TM data (the thermal channel TM6 was not included in the processing):

(1) Radiometric correction—this is the conversion of the TM 8-bit digital numbers into physical quantities of radiance and reflectance, and followed Markham and Barker 1986 and Thome et al. 1997.

(2) Atmospheric corrections were carried out to overcome the degradation of the target reflectance signal caused by scattering and absorption by aerosols and water vapour in the atmosphere (Fraser and Kaufmann 1985, Kaufmann 1988). The top-of-atmosphere (TOA) reflectance values were calculated for all images. Unfortunately, no data about the atmosphere were available for the 1987 images and the correction for water vapor and aerosol content in the atmosphere was not carried out. The Landsat images from 1987 were only corrected for Rayleigh scattering and ozone content, which mainly occurs in the visible channels of the TM sensor. Ozone does not vary in time and space and therefore monthly values can be used. In such situations Teillet and Fedosejevs (1995) suggest a dark target approach. This approach was applied for the 1987 images. Based on the dark surfaces in the Makhtesh Ramon (basalt hills), which are stable and not covered by vegetation. Spectral variability in all wavelengths between the images was checked. All images show a low variability. The differences between the atmospherically corrected and uncorrected vegetation indices for the basalt hills (where atmospheric impacts are expected to be the greatest) were minor (<1%). We concluded that water vapor and aerosol content in the atmosphere during acquisition of the Landsat TM data 1987 were very small. Consequently, and after a visual interpretation of the 1987 images revealed they were very clear without any atmospheric “noises", we decided the 1987 images could be compared with the atmospheric corrected 1995 images. Measurements of aerosol and water vapour content were available for the 1995 images from a ground measurement station in Sede Boqer. Estimates of total precipitable water and aerosol properties of the atmosphere were obtained from an automatic sun tracking photometer at Sede Boqer. Atmospheric correction of the TOA reflectance was carried out using the 6S algorithm (Vermote et al. 1996). In this study, we also used the 6S code to calculate the TOA reflectance for the 1987 TM images.

(3) Geometric corrections—were done so that the Landsat TM data had the same geometrical information as the ground observations (Jensen 1986). These errors were corrected using Ground Control Points (GCPs) on the surface of the earth where both image coordinates and map coordinates could be identified with acceptable accuracy. All 4 Landsat-TM images were rectified based on 23 well-distributed control points. We used a first order polynomial equation to convert the file coordinates to rectified map coordinates. The new rectified images were resampled with the nearest neighbor resampling method to a pixel size of 30 m.

Satellite Data Analysis

Many different methods exist for reducing background influence on vegetation indices (VIs). We selected and compared 5 VIs from 2 groups that characterise the vegetation cover. The first group are VIs based on the Red/Near-infrared (R/NIR) slope. This group of VIs is used when there are strong influences of soil (background) brightness on vegetation indices, and special VIs must be applied in order to reduce the background noises (Huete 1986, Huete and Jackson 1987). From this group we selected 3:

(1) Normalized Difference Vegetation Index (NDVI - Rouse et al. 1974), where:

$$NDVI = \frac{(NIR - R)}{(NIR + R)} \quad \textbf{(1)}$$

(2) Soil Adjusted Vegetation Index (SAVI—Huete 1988) is defined by an additional soil adjustment factor (*L*). In our case, we defined *L* = 1, because of the sparse vegetation cover.

$$SAVI = [\frac{(NIR - R)}{(NIR + R + L)}] *2. \quad \textbf{(2)}$$

(3) Modified SAVI (MSAVI—Qi et al. 1994) is a modification of the SAVI, where the factor *L* is not constant and varies inversely with the amount of vegetation present.

$$MSAVI = \frac{2NIR + 1 - \sqrt[2]{(2NIR + 1)^2 - [8(NIR - R)]}}{2} \quad \textbf{(3)}$$

The second group of VIs we used is based on the perpendicular distance in relation to the bare soil line. From this group we selected 2:

(1) Perpendicular Vegetation Index (PVI—Richardson and Wiegand 1977), where:

$$\mathrm{PVI} = \frac{(NIR - aR - b)}{\sqrt[2]{a2 + 1}}$$

and *a* and *b* are the slope and intercept of the bare soil line.

(2) Transformed SAVI (TSAVI–Baret et al. 1989).

$$\mathrm{TSAVI} = \frac{[a(NIR - aR - b]}{(\mathrm{R + aNIR - ab})}$$

where *a* and *b* are the slope and intercept of the bare soil line.

The bare soil line for the Makhtesh Ramon cirque was estimated by means of the reflectance values in the red band (TM3) regressed against the means in the near-infrared band (TM4) of selected bare surfaces inside the cirque.

Ground Measurements and Comparison to Satellite Data

To test our ability to detect differences in vegetation cover and grazing impact through satellite imagery we compared our satellite data with ground measurements. We carried out 2 separate series of ground measurements to assess whether:

(1) we can detect changes in plant community structure through satellite data, and

(2) we can detect differences in vegetation cover (grazing pressure) through satellite data.

In the first series we sampled 8 circular plots with a 26 m diameter located along the long axis of the cirque, following the most significant environmental gradient, altitude (Ward et al. 1993). This is an effective means of sampling the maximum potential variation in plant-species composition in large areas and captures more information about vegetation attributes than randomly placed plots similar size (Gillison and Brewer 1985). In the second series we divided the cirque into 3 areas along the altitudinal gradient: western, central and eastern, and paired them with 3 parallel areas south of the cirque in the Nekorot riverbed. In each area we sampled 5 circular plots with a 26 m diameter. We sampled these areas twice, at the end of the rainy season (March 1995) and at the end of the dry season (September 1995). From personal observations of Asiatic wild ass behavior we knew that they spent far more time grazing/browsing in the 3 areas inside the cirque than in the 3 areas outside. Thus, our comparisons were made between plots with high and low herbivory, respectively.

We used the log-series survey sampling method to quantify plant density and cover of perennial vegetation. This method is appropriate for use in arid environments where perennial ramets are fairly distinct and separate (McAuliffe 1990, Ward et al. 1993). Numbers of individual ramets for each species within a plot are assessed. These numbers are used to assign species to logarithmic density classes equivalent to the logarithmic (base 2) values of actual abundances. The species is assigned to a $\log_2$ canopy class based on the median canopy diameter of the species in the plot. Log_2 total cover per plot is determined by adding logarithmic density and cover classes. Percent cover is derived by taking the antilog of the difference between $\log_2$ cover per species and $\log_2$ total plot area. We carried out 2 separate sets of measurements. In the first set we selected 8 plots along the altitudinal gradient within the Ramon cirque. In the second we carried out, within each of the 6 areas (3 inside and 3 outside the cirque) mentioned above, 5 McAuliffe plots that were placed within 30 m of one another on the same substrate.

Plant species richness was defined as the number of species per McAuliffe plot. We used Shannon-Wiener's index of species diversity from the plot data, following Magurran (1988). Ordinations of community structure was done by Detrended Correspondence Analysis (DECORANA). This is an improved eigenvector technique based on reciprocal averaging (also called correspondence analysis) but correcting its main faults (Hill and Gauch 1980). Reciprocal averaging (RA) can be viewed geometrically as the derivation of new axes which maximally account for the structure of points (=sample plots or species) in a multidimensional cloud of points, making possible the reduction of dimensionality. Algebraically, RA uses simple matrix algebra to obtain reciprocal weighted averages of sample and species scores by iteration. These weighted averages are used for ordinating samples and/or species. The 2 main faults of reciprocal averaging are:

(1) The undesirable 'arch' effect that occurs in second and higher order axes. This arch is undesirable because it causes a systematic relationship between the second and first axes.

(2) The compression of the first axis ends relative to the middle so that a given distance of separation in the ordination does not have a consistent meaning in terms of implied differences between samples or species (Gauch 1982). DECORANA is so-named because it detrends the undesirable arch effect that occurs in second and higher order axes in reciprocal averaging (Gauch 1982). DECORANA is an indirect ordination technique and, as such, ordinations of samples with particular environmental variables must be done after the ordination values have been obtained. In practice, this process involves regressing ordination scores on 1 or several axes with each environmental variable in turn.

To validate our observations on Asiatic wild ass activity, we estimated the degree of herbivory and intensity of habitat. Degree of herbivory was estimated in the McAuliffe plots mentioned above by recording the degree of herbivory on 5 plants from each of the 5 most abundant plant species. We ranked each plant according to the degree of herbivory as 0= no herbivory; 1= <50% of external branches eaten, and 2=> 50% external branches eaten. We indexed intensity of habitat use by faecal counts. Density of faecal piles was recorded on 5 parallel 250 m-long transects walked along Asiatic wild ass routes of travel in each of the six areas. Perpendicular distance to each pile was recorded along the length of the transect. Density was calculated using distance sampling techniques (Buckland et al. 1993).

We compared satellite data to ground measurements by standard regression procedures. We did separate regression for each of the 5 vegetation indices (VIs). For the first series we selected 8 sub-sections of 3×3 pixels (90×90 m), each sub-section covering one of the ground measurement plots. We ran regressions with VIs derived from dry season (September 1995) and wet season (March 1995) TMs. For the second series we selected randomly, from each of the 6 areas, 3 sections of 3×3 pixels from the same Thematic Mapper section TMs in the general areas of the 5 ground measurement circular plots. We regressed the mean VIs of the 3 sections in each area on the mean cover calculated from the 5 circular plots.

Results

Satellite Data Processing

The influence of the atmospheric correction on the reflectance values in Thematic Mapper™ channels 1–5 and 7 indicate that deviations vary with surface type (Table 1). In 5 of the 6 wavebands, corrected values deviated significantly from uncorrected values ($P<0.05$, sign test). Changes in the reflectance value after the atmospheric correction were the greatest in the blue waveband (TM1) the near- and middle infrared bands (TM4-5, 7). This is mainly caused by molecular and aeroscattering in the blue band and water vapour absorption in the near- and middle infrared bands. In the blue waveband (TM1) the correction resulted in a decrease of the reflectance value, especially for areas with dense vegetation cover and dark surface colour. In the near-infrared waveband (TM4), water vapour absorption is responsible for the magnitude of the correction. The difference between TM3 and TM4 (red-near-infrared) increased after the atmospheric correction. The atmospheric effects are less important over bright surfaces with less vegetation cover. After rainfall, when all different vegetation components respond photosynthetically and the bright desert surface changes to a darker surface, the effects of atmospheric noises increased. Slope and intercept of the bare soil line were 1.305 and 0.0313 ($r^2=0.991$), with basalt at the lower end and gypsum at the upper end.

Table 1. Average Delta (atmospheric corrected and uncorrected reflectance values) for different surface types.

	TM1	TM2	TM3	TM4	TM5	TM7
Spring image 1995 (03/95)						
Area with dense vegetation	-0.017	0.002	0.006	0.026	0.031	0.026
Basalt (dark surface type)	-0.025	-0.017	0.009	0.006	0.006	0.002
Gypsum (bright surface type)	-0.013	0.010	0.015	0.028	0.035	0.028
Fall image 1995 (09/95)						
Area with dense vegetation	-0.007	0.009	0.012	0.025	0.035	0.039
Basalt (dark surface type)	-0.011	-0.003	0.002	0.009	0.012	0.012
Gypsum (bright surface type)	-0.004	0.015	0.017	0.029	0.040	0.037

Ground Measurements and Vegetation Indices

In the first series the Standard Deviation of the 9 pixels from the TM image in each subsection was very small. Therefore, the areas can be considered as very homogeneous and suitable for a comparison with the ground measurements. However, although coefficient of variation (CV) for the cover estimation in the 8 plots using the ground measurements were high (CV=0.381, range=20.0–77.8%), none of the vegetation indices (VIs) used correlated well with ground measurements (Table 2). The Normalized Difference Vegetation Index (NDVI) and the Transformed Soil Adjusted Vegetation Index (TSAVI) had the highest correlation between percent vegetation cover and VI value, albeit non-significant ($R^2=0.471$, $P=0.060$ and $R^2=0.471$, $P=0.059$, respectively).

In the second series, we found no relationship between ground measurements and the satellite data, with $R^2 \leq 0.1$ for all VIs. However, based on our ground measurements, percent vegetation cover was significantly higher in Nekorot dry riverbed outside the cirque than along the Ramon riverbed inside the cirque (15.8±1.5 vs. 11.2±0.9, $P<0.016$). The results were consistent for each of the 3 areas (10.4±1.7 vs. 17.3, 11.9±1.7 vs. 15.3±2.4, and 11.2 vs. 15.8 for the west center and east, respectively) with no significant difference in the ground measurements between the east center and west areas. Density of Asiatic wild ass dung piles was 74.4±19.8/ha inside the cirque as compared with 15.0±9.5/ha outside the cirque (P=0.022). The median index of herbivory was 1, 2 and 1 for the east, center and west areas inside the cirque and was 0 for all areas outside the cirque. To make sure that differences in ground measurements were not due to differences in species composition, we calculated the Morisita-Horn index of plot similarity (Magurran 1988) for comparison made between plots inside to those outside the cirque and within plots inside and outside the cirque. Similarity between plots inside and outside the cirque was 1.18± 0.42, 1.46±0.25, and 1.32±0.43 for the west, center and eastern areas, respectively, and did not differ from the 'within' indices (1.32±0.39, 1.56±0.33, and 1.38±0.47, P=0.251, 0.260, and 0.681, respectively).

Table 2. Correlation of vegetation indices with percent vegetation cover determined by ground measurements.

Index	Dry season	Wet season	Seasonal variation
	R^2	r^2	r^2
NDVI	0.227	0.471	0.048
SAVI	0.005	0.003	0.033
MSAVI	0.001	0.003	0.004
PVI	0.109	0.326	0.019
TSAVI	0.212	0.473	0.124

Table 3. Analysis of variance for the TSAVI vegetation index (after an arcsin transformation) comparing seasons (dry vs. wet), areas (west, center and east parts of the study area) and grazing status (grazed vs. ungrazed). 1987 and 1995 were analyzed separately.

1987	Source	DF	F value	P
	Season	1	50.4	0.0001
	Area	2	4.9	0.015
	Grazing status	1	5.2	0.030
	Season * Grazing status	1	4.41	0.045
1995	Source	DF	F value	P
	Season	1	79.8	0.0001
	Area	2	7.7	0.002
	Grazing status	1	8.3	0.008
	Season * Grazing status	1	7.0	0.014
	Area * Grazing status	2	8.6	0.001

Analyses of variance for the best performing VIs (TSAVI and NDVI) were carried out separately for 1987 and 1995 using season, area (east, center or west) and grazing status (in and out of the cirque) as predictors. In 1987 only the effect of season and grazing status were significant with no significant interactions (Table 3). The mean VI value was 10% higher outside the cirque in both seasons. In 1995, grazing status and area were significant (Table 3), as well as the interaction between season and grazing status and area and grazing status. Mean VI during the wet season was 10% higher in the grazed area (inside the cirque) during the wet season, but declined in the dry season to the same level as the ungrazed area (Fig. 2).

Discussion

Our ground measurements showed that there was a 30% decline in vegetation cover from the grazed to the ungrazed area (from 15.8% to 11.2%). However, we were unable to correlate vegetation indices (VIs) from satellite imagery to these values. An ANOVA on the VIs from the 1995 Thematic Mappers (TMs) produced a significant interaction between season and grazing status with cover declining more in the grazed area from the wet to the dry season. No such pattern was evident in the 1987 TM data. This may be indicative of increased grazing pressure in recent years inside the cirque. However, 1987 was a dry year and is, therefore, a weak control. Regretfully, there are no clear TM images from wet years at the early stage of the reintroduction (1987 and earlier).

Strong differences in VIs were found between seasons and years suggesting that changes in vegetation due to rainfall patterns can be detected. The absence of a clear difference between grazed and ungrazed areas using VIs may be due to the low ground cover that typifies hyper-arid environments. In our case a decline of 30% in ground cover is associated with an absolute decline of only 15.6–11.2=4.6%. Makhtesh Ramon cirque is characterised by a heterogeneous geology, which is covered by sparse vegetation (Ben-Dor et al. 1995, Kaufmann 1988, Ward et al. 1993). Therefore, the background colour and brightness has a much greater impact on the vegetation index than over a homogeneous surface. Thus, the 'noise' caused by the high variance in soil reflectance combined with highly variable rainfall patterns may overshadow any grazing effects that might exist. This result is consistent with the conclusion of Ezra et al. (1984) that satellite derived VIs may be less useful in arid than in mesic envi-

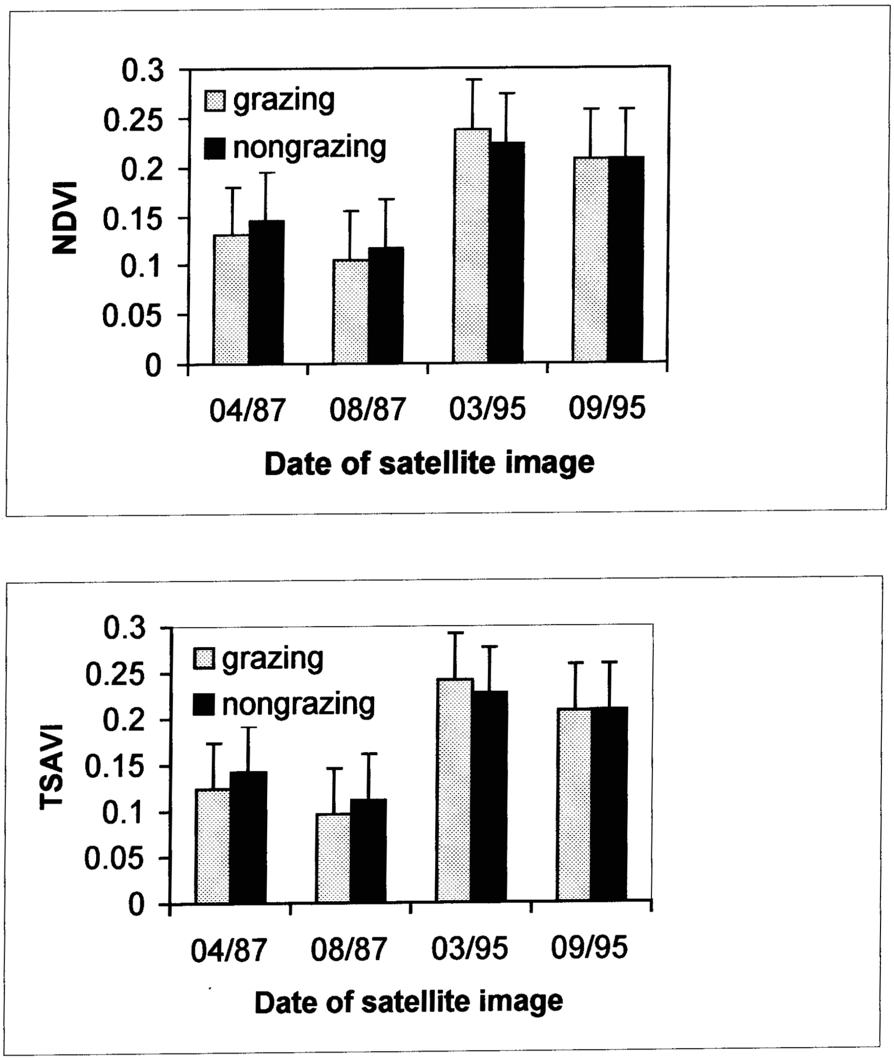

Fig. 2. Mean Vegetation Indices (VIs) for Normalized Difference Vegetation Index (NDVI) and Transformed Soil Adjusted Vegetation Index (TSAVI) for year, season and comparing grazed and ungrazed areas.

ronments due to the influence of soil background on the radiometric signal.

We conclude that although grazing impacts may exist, at their current levels we are unable to detect them via satellite imagery. This is problematic because while an absolute decline in vegetation cover of 5% may be negligible in wetter areas with 50% cover, in areas with 10-15% cover this constitutes a considerable reduction in carrying capacity. The significant interaction between grazing status and season in 1995 suggests that it may be possible to detect small changes in cover, but this level of change is not sufficient as a direct index of existing ground cover. However, to use changes in ground cover, a baseline pattern must be established (such as a TM from a wet year prior or shortly after the first reintroduction).

The difference between TM3 and TM4 (Δred–near-infrared) increased after the atmospheric correction. This change is important for the calculation of vegetation indices, which are based on the red and near-infrared part of the spectrum. The atmospheric effects are typically less important over bright surfaces with less vegetation cover. After rainfall, when all different vegetation components respond photosynthetically and the bright desert surface changes to a darker surface, the effects of atmospheric "noises" increased. These results emphasise the importance of the atmospheric effects (molecular and aerosol scattering, and water vapour absorption) in Landsat TM measurements of surface reflectance in a desert environment. The importance and accuracy required of atmospheric correction depends on the purpose for which the data are to be used. Studies based on satellite data for comparison of different areas or satellite data acquired at different times should consider, and correct for, the "noise" effect of the atmosphere.

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J. Range Manage.
52:508–514 September 1999

Intake of cattle offered normal and lodged tall fescue swards

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Abstract

Grazing behavior of livestock may be altered when grass swards are lodged by trampling or wind and rain. We used a balanced change-over design to investigate the effects of lodging on the ingestive behavior of Angus cows (*Bos taurus* L.)(mass (M): 344 kg) grazing swards of vegetative endophyte-free 'Kenhy' tall fescue (*Festuca arundinacea* Schreb.). Animals were offered normal swards (T_1), lodged swards (T_2), or swards with one half of their area lodged (T_3). To simulate lodging, swards were covered overnight with weighted plywood sheets that compressed sward surface height (SSH) from 34 to 14 cm and elevated sward dry matter (DM) density from 151 to 499 kg ha^{-1} cm^{-1} for herbage > 5 cm. Mean herbage DM intake per bite was 561 mg for T_1, 713 mg for T_2 and 792 mg for T_3. Cattle grazed at 28 bites min^{-1} for T_1, and 25 bites min^{-1} for both T_2 and T_3. Herbage DM intake rates were 0.27, 0.31, and 0.33 kg 100 kg^{-1} (M) hour^{-1} for T_1, T_2, and T_3, respectively. In another experiment, cattle were offered equal areas of normal swards (SSH: 27 cm) and lodged swards (SSH: 16 cm), normal and partially defoliated swards (SSH: 20 cm) swards, or lodged and partially defoliated swards. When offered normal and lodged swards, 64% of DM intake came from normal swards. When offered normal and partially defoliated swards about 60% of DM intake came from normal swards. Cattle grazed equally on lodged and partially defoliated sward segments when offered that choice.

Resumen

El comportamiento del ganado en apacentamiento puede ser alterado cuando las praderas están acamadas por pisoteo, viento o lluvia. Utilizamos un diseño balanceado "change-over" para investigar los efectos del acame en el comportamiento ingestivo de vacas Angus (*Bos taurus* L.)(masa (M): 344 kg) apacentando praderas alta fescue (*Festuca arundinacea* Schreb.) var 'Kenhy' en estado vegetativo libres de endofito. A los animales se les ofreció pradera normal (T1), praderas acamadas (T_2) o praderas con la mitad de su área acamada (T_3). Para simular el acame, las praderas se cubrieron durante toda la noche con hojas de madera que comprimieron la altura de la superficie de la pradera (ASP) de 34 a 14 cm y elevaron la densidad de la materia seca de la pradera de 151 a 499 kg ha^{-1} cm^{-1} para el forraje > a 5 cm. La media de consumo de materia seca de forraje por bocado fue de 561 mg para el T_1, 713 mg para el T_2 y 792 mg para T_3. El ganado apacentó a un ritmo de 28 mordidas min-1 en el T_1, y 25 mordidas min-1 en el T_2 y T3. Las tasas de consumo de materia seca de forraje fueron 0.27, 0.31 y 0.33 kg 100 kg^{-1} (M) hr^{-1} para los tratamientos T_1, $T_{2,}$ y T_3 respectivamente. En otro experimento, se le ofreció al ganado áreas iguales de pradera normal (ASP: 27 cm), pradera acamada (ASP: 16 cm) y pradera normal y parcialmente defoliada (ASP: 20 cm) o praderas acamadas y parcialmente defoliadas. Cuando se ofreció praderas normales y acamadas 64% del consumo de materia seca provino de la pradera normal. Cuando se ofrecio al ganado pradera normal y parcialmente defoliada aproximadamente 60% del consumode materia seca provino de la pradera normal. El ganado apacentó en forma similar cuando se le ofrecieron a elección propia segmentos de praderas acamadas y parcialmente defoliadas.

Key Words: Grazing behavior, ingestive behavior, diet selection, herbage density, sward surface height.

Surface height and bulk density of pastures are involved in the determination of the amount and rate of intake of grazing animals (Ungar et al. 1991, Hodgson et al. 1994). These sward properties are among several that are altered by activities of grazing livestock, by vehicular and human traffic, and by lodging (Edmonds 1964, Abdel-Magid et al. 1987, Dougherty et al. 1989a, Guthery and Bingham 1996, Sheath and Carlson 1998). Lodging of swards by wind and rain is significant in tall fescue (*Festuca arundinacea* Schreb.) accumulated for hay or deferred grazing (Taylor and Templeton 1976). Information about lodging effects on processes of ingestion and on diet selection is needed for research in grazing management and the development of simulation models of grazing systems (Bailey et al. 1996, Herrero et al. 1998, Loewer 1998).

To establish the effects of lodging on herbage intake of cattle, we compared grazing of normal swards with grazing of swards that had been compressed to simulate lodging. We also compared herbage intake of cattle offered a choice of normal or compressed swards, normal or partially defoliated swards, and compressed or partially defoliated swards.

This research was supported by Project KY99002 of the Kentucky Agricultural Experiment Station. This paper is published with the approval of the Director, Kentucky Agricultural Experiment Station as Journal Paper 98-06-135.

Manuscript accepted 14 Dec. 1998.

Materials and Methods

Experiment Design and Statistical Analysis

We used a 4-period change-over design for 3 treatments and 12 animals previously described (Dougherty et al. 1987, 1989b). This design was constructed by concatenating 3 Quenouille-Berenblut 4 x 4 change-over designs (Quenouille 1953, Berenblut 1964, 1967). The 2 treatments assigned to each 4 x 4 square being 1 of 3 possible pairs of 3 treatments. Columns (i.e. animals) in the resulting 4 x 12 design constitute a balanced incomplete block design. Rows (i.e. days) of the design are complete blocks containing each of the 3 treatments 4 times. The sequencing of treatments within each column (i.e. animals) is such that the design is balanced for first residual effects.

In Experiment I (Exp. I), the 3 treatments were normal swards (T_1), compressed swards (T_2), and swards in which half was normal and the other half compressed (T_3) (Table 1). In one treatment (T_1) of Experiment II (Exp. II), cattle were offered plots with one half of the sward compressed (Table 1). In the second treatment (T_2), cattle were offered plots with one half cut to 20 cm above the soil surface and the herbage removed. In the third treatment (T_3), cattle were offered plots with one half of the sward surface area compressed and one-half cut to 20 cm, as in T_1 and T_2, respectively.

The statistical model was:

$$Y_{ijkm} = \mu + A_k + D_m + T_i + \delta R_j + \varepsilon_{ijkm} \quad (1)$$

where Y_{ijkm} is the mth day measurement taken on the kth animal that received the ith treatment on the mth day and the jth treatment on the (m-1)th day; μ is the overall mean, A_k is the effect of the kthanimal, D_m is the effect of the mth day, T_i is the direct effect of the ith treatment, $\delta = 1$ if $m>1$, zero otherwise, and R_j is the residual (carryover) effect of the jth treatment. The random errors, ε_{ijkm}, are assumed NID (0, δ^2). Data were analyzed with the General Linear Models procedure of SAS Institute Inc. (1997).

Pasture Management

We used a monoculture of 'Kenhy' tall fescue that had been established in spring 1988 on Maury silt loam (fine, mixed, mesic Typic Paleudalf) on the Spindletop research farm of the Kentucky Agricultural Experiment Station (38°07'59"N 84°29'58"W) (Table 2). The field was managed in accordance with current Kentucky recommendations for soil fertility and weed and pest control for beef cattle production (Henning and Lacefield 1991). First growth herbage was cut at 5 cm and harvested as hay on 11 May. Urea-N was applied at 50 kg ha^{-1} on 21 May.

Sward compression treatments were applied during the afternoons on the day before plots were scheduled for grazing. In Exp. I, circumferences of 4 m^2 plots were delineated by cutting 55-cm wide rings to a height of 5 cm with a mower tethered to pivots located at plot centers. Two sheets of plywood (1.27 x 122 x 244 cm) were laid on sward surfaces of each plot assigned to the compressed sward treatment (T_2). One plywood sheet was laid on one half of each plot assigned to the half normal-half compressed treatment (T_3). Each plywood sheet was weighted with 2 steel rods, each weighing about 5 kg. Plywood was removed each morning just before cattle were introduced to the experimental swards.

Grazing area of plots were 15 m^2 in Exp. II. Each plot was dissected by mowing a 50 cm wide diameter strip. One half of each normal (T_1) and T_3 plot was compressed overnights with weighted plywood sheets, as in Exp. I. For cut halves of T_2 and T_3 plots, herbage was severed and collected with a 50 cm wide rotary mower mounted on rails 20 cm from the soil surface, herbage was dried to a constant weight at 75°C (DM removed: 1.01 ± 0.26 kg per plot; 674 ± 166 kg ha^{-1}). Cutting treatments were imposed each morning immediately before grazing commenced.

Animal Management

Twelve adult Angus cows (mean body mass (M): 344 ± 24 kg), which were experienced in tethered grazing and neither pregnant nor lactating, were used in both experiments. When cattle were not grazing, they were kept in a shaded drylot with unlimited access to water. Cattle were placed on experimental grazing plots at 0900 hours EDT and removed at 1000 hours EDT. At 1300 hours EDT, cows were released for free-range grazing on Kenhy tall fescue pastures and at 1500 hours EDT they were returned to their drylot. Overall management of cows was in accordance with current Kentucky recommendations for nutrition and health of non-pregnant, non-lactating adult cows (Burris and Johns 1991). In Exp. I, mean herbage dry matter (DM) allowance (>5 cm) was 1.74 ± 0.14 kg animal^{-1} hour^{-1}. In Exp. II, herbage DM allowances for the 1-hour grazing period were 7.85 ± 0.77 kg (T_1), 6.95 ± 0.73 kg (T_2), and 6.51 ± 0.64 kg

Table 1. Treatments, sward characteristics, herbage allowances and other initial conditions of Exp. I and Exp. II.

Condition	Exp. I	Exp. II
Treatment 1	Normal swards	Normal/compressed swards
Treatment 2	Compressed swards	Normal/cut swards
Treatment 3	Normal/compressed swards	Compressed/cut swards
Measurement phase	0900–1000 EDT 2–6 July 1990	0900–1000 EDT 10–13 July 1990
Plot area	4 m^2	15 m^2
Herbage DM content	234 ± 20 g kg^{-1}	236 ± 56 g kg^{-1}
Herbage DM mass	4,247 ± 357 kg ha^{-1}	5,100 ± 745 kg h^{-1}
Sward surface height	Normal: 34.2 ± 3.7 cm Compressed: 14.3 ± 3.4 cm	Normal: 27.0 ± 3.4 cm Compressed: 15.7 ± 3.7 cm Cut: 20.0 ± 2.6 cm
Herbage DM density	Normal: 151 ± 21 kg ha^{-1} cm^{-1} Compressed: 499 ± 155 kg ha^{-1} cm^{-1}	Normal: 246 ± 61 kg ha^{-1} cm^{-1} Compressed: 386 ± 191 kg ha^{-1} cm^{-1} Cut: 264 ± 65 kg ha^{-1} cm^{-1}
Extended tiller length	48 ± 6 cm	Normal: 54 ± 7 cm Cut: 23.3 ± 2 cm
Tiller DM mass	436 ± 80 mg	434 ± 113 mg
Pseudostem length	8.9 ± 1.5 cm	0.9 ± 1.5 cm
DM allowance	1.74 ± 0.14 kg	T_1: 7.85 ± 0.77 kg T_2: 6.95 ± 0.73 kg T_3: 6.51 ± 0.64 kg

Table 2. Location, soil type, experiment design, pasture and animal features common to both Exp. I and Exp. II.

Conditions	Information
Location	Spindletop Farm, Fayette County, Kentucky. Ky Agric. Exp. Sta.
Coordinates	38°07’59”N 84°29'58”W
Soil type	Maury silt loam (fine, mixed, mesic Typic Paleudalf)
Plant species	*Festuca arundinacea* Schreb. cv Kenhy, endophyte-free
Design	Three integrated 4 x 4 change-over designs balanced for first residual effects
Animals	*Bos taurus* L. Adult angus females, non-pregnant, non-lactating Body mass (M): 344 ± 24 kg

(T_3); less in T_2 and T_3 because one half of plots were defoliated to 20 cm.

Measurements

Trained observers (one observer per 4 animals) used sound and sight to determine and count prehension bites of each animal sequentially for 1 min each during measured grazing meals (Dougherty et al. 1987). On divided plots, observers recorded the number of bites taken by cattle from each sector of normal, compressed, or cut swards. Sward surface heights were measured with a height stick at 10 sampling sites at 0.5 m distances about 20 cm inside circumferences, before swards treatments were applied, after sward treatments were applied, before grazing commenced, and after cattle were removed from swards.

On each of the 4 days of measurement, herbage of 14 ungrazed control plots, 2 tangential to each grazed plot, and the residual herbage of the 12 grazed plots was cut (>5 cm) and weighed with a 1.5 m sickle bar harvester. Samples of herbage were dried to a constant weight at 75°C to estimate herbage DM content. Lengths of pseudostems and extended lengths of tillers were measured on 10 tillers per plot sampled from plots before and after grazing at fixed intervals 10 cm in from the circumference.

Herbage dry matter (DM) allowances were estimated from the mean herbage DM mass (>5 cm) of 2 tangential ungrazed control plots (each 6 x 1.5 m). Herbage DM intake per animal was estimated from the difference between the herbage DM offered and the residual herbage mass of each grazed plot. Herbage DM utilization was estimated from herbage DM intake and herbage DM allowance. Herbage DM intake per bite was derived by dividing herbage DM intake by the product of grazing time and mean rate of biting. Dry matter density of swards was estimated from the sward surface height (>5 cm) and herbage DM mass (>5 cm). Bite volumes were calculated from bite masses and DM densities of herbage in the grazed horizons.

Weather

Selected weather variables (Table 3) during the measured grazing periods were obtained from the Spindletop weather station, which is within 50 m of the site of the experiment, and operated by the Agricultural Weather Center of Kentucky Agr. Exp. Sta., according to specifications of the National Weather Service. Sward surface temperatures during grazing sessions were recorded with an infrared thermometer.

Results

Experiment I

At the start of Exp. I, herbage dry matter (DM) mass (>5 cm) of normal (unmodified) swards was 4,247 ± 357 kg ha^{-1} (Table 1). Compression of the sward overnight with weighted plywood significantly lowered the sward surface height from 34.2 ± 3.7 to 14.3 ± 3.4 cm and increased sward DM density from 151 ± 21 to 499 ± 155 kg ha^{-1} cm^{-1}. Weather was normal during measured grazing meals.

No significant ($P>0.05$) first residual effects of the sward compression treatments were revealed by analysis of variance and, as a consequence, only least squares means of direct effects of treatments on ingestive behavior are presented (Table 4).

The ingestive behavior of cattle during measured grazing meals was altered by sward compression. Cattle grazed compressed swards (T_2) and swards that were half-compressed (T_3) faster than they grazed normal swards (T_1) but only the contrast between normal swards and half-compressed swards (T_3) reached significance ($P=0.03$).

Herbage DM mass per bite was significantly higher for compressed (T_2) ($P=0.02$) and half-compressed swards (T_3) ($P<0.01$) than for normal swards (T_1). The one-third greater DM mass of bites taken by cattle grazing from compressed swards was associated with an increase in sward DM mass density from 151 to 499 kg ha^{-1} cm^{-1}. It is also apparent that cattle offered compressed swards prehended and severed the herbage of about one-third of the volume of that of cattle offered normal swards. Cattle grazing compressed swards (T_2 and T_3) prehended and severed 3 bites min^{-1} fewer ($P=0.10$) than cattle offered normal swards.

Sward surfaces before grazing were 34 cm above the soil surface for normal swards and 14 cm above the soil surface for compressed swards. After grazing, sward surface height above the soil surface was about 16 cm for normal swards and nearly 14 cm for compressed swards.

With the design used we could not differentiate the relative amount of herbage DM intake from normal and compressed swards in the T_3 treatment. Cattle offered split swards exhibited similar behavior to

Table 3. Canopy surface temperatures and weather data from the Spindletop weather station during measured grazing meals for Exp. I and Exp. II.

Variable	Exp.	Day 0	Day 1	Day 2	Day 3	Day 4
Dates I	I	1 July	2 July	3July	4 July	5 July
	II	9 July	10 July	11 July	12 July	13 July
Air temperature (°C)	I	26.9	28.0	25.6	28.6	25.6
	II	30.6	29.4	27.8	21.4	19.2
Canopy temperature (°C)	I	—	21.5	23.4	27.2	24.4
	II	—	29.7	27.2	21.2	21.2
Relative humidity (%)	I	66	65	58	75	67
	II	66	72	70	81	93
Solar radiation (MJ m^{-2})	I	1.945	1.799	2.197	1.695	2.113
	II	2.029	1.966	1.841	0.16	0.335

Table 4. Least squares means of selected sward variables after grazing and variables of grazing behavior of beef cattle grazing normal (T_1), compressed swards (T_2), and split (normal/compressed swards) (T_3) (Exp. I).

		- - - - - - - - - - - - - Treatment - - - - - - - - - - - - -			- - - - - - - - - - - - -Contrast- - - - - - - - - - - - -		
Variable	Units	T_1: normal	T_2: compressed	T_3 split	T_1 vs T_2	T_1 vs T_3	T_2 vs T_3
					- - - - - - - - - - - -(Probability)- - - - - - - - - - -		
Residual DM	(kg ha^{-1})	2,038	1,661	1,518	0.08	0.17	0.49
Sward DM	(g kg^{-1})	255	263	262	0.40	0.43	0.97
Sward surface	(cm)	16.2	13.7	13.8	0.02	0.02	0.93
DM utilization	(%)	52.2	60.2	63.4	0.11	0.03	0.50.
DM intake rate	(kg hour^{-1})	0.918	1.047	1.128	0.18	0.03	0.39
	(kg 100 kg^{-1} hour^{-1})	0.268	0.306	0.328	0.18	0.04	0.41
Biting rate	(bites min^{-1})	27.8	24.7	24.8	0.10	0.11	0.97
DM intake per bite	(g)	0.561	0.713	0.792	0.02	0.01	0.24
Sward bite volume	(liters)	1.449	0.559	0.467	0.01	0.01	0.31
Sward bite density	(g liter^{-1})	0.324	1.728	1.949	0.002	0.001	0.60

those offered compressed swards (T_2). About 54% of bites recorded for cattle assigned to the split swards were taken from the normal segment ($P>0.05$). The higher mean bite mass of animals assigned to split swards ($P<0.01$), may indicate that more of the total ingesta came from the compressed sector.

In summary, sward compression increased sward DM density 3-fold but resulted in only small increases in rate of herbage DM intake. Herbage DM intake per bite increased less than anticipated for cattle grazing compressed swards because the increase in DM density was associated with a 3-fold decrease in the volume of herbage prehended and severed. Slightly slower rates of biting of cattle grazing compressed swards also partially countered the effect of sward DM density on DM density per bite.

Experiment II

Herbage dry matter (DM) mass (>5 cm) in normal (unmodified) swards was 5,100 ± 745 kg ha^{-1}, sward surfaces was 27 ± 3.4 cm, and herbage DM density (> 5 cm) was 246 ± 61 kg ha^{-1} cm^{-1} (Table 1). Compression of swards overnight lowered sward surfaces to 15.7 ± 3.7 cm and raised herbage DM density (>5 cm) to 386 ± 191 kg ha^{-1} cm^{-1}. When normal swards were cut to 20 cm, herbage DM mass (>5 cm) was depleted by 674 kg ± 166 kg ha^{-1} while herbage DM density (>5 cm) increased to 264 ± 65 kg ha^{-1} cm^{-1}.

There were no significant residual effects ($P>0.05$) of the sward treatments in Exp. II, consequently, only least squares means of direct effects of treatments on relevant variables are presented (Table 5).

Cattle offered normal/cut swards (T_2) ingested 2.49 kg of herbage DM during 1 hour of grazing, while those grazing normal/compressed swards (T_1) ingested 1.99 kg, and those offered compressed/cut swards (T_3) ingested 2.06 kg. Herbage DM intake by segments of normal/compressed plots (T_1) indicates that normal swards accounted for about 64% of DM intake. Intake data from normal/cut plots (T_2) shows that cattle preferred normal swards to cut swards by a ratio of 60:40. Cattle showed only slight preference for compressed swards in terms of DM intake when offered compressed/cut swards (T_3). Analysis of variance also indicated some variation in preference between animals ($P=0.09$) and between days ($P=0.03$).

One-third or less of the herbage DM allowance was consumed by grazing cattle. This indicates that intake was not limited by availability of herbage, even when cattle grazed the cut segments of T_2 and T_3 plots where herbage DM allowances were lowered by the removal of about 1 kg of herbage DM.

In terms of the proportion of bites taken from each sector, cattle took 74 and 79% of bites from normal segments when offered the choice of normal/compressed swards (T_1) or normal/cut swards (T_2), respectively. They took similar numbers of bites from each segment of compressed/cut swards (T_3).

Estimated mean herbage DM mass per bite was 1.1 g for cattle grazing normal sward segments (T_1 and T_2) and 1.6 g per bite for cattle grazing compressed swards (T_3) ($P<0.05$). We were unable to estimate bite mass of animals grazing the 'B' segments (compressed, cut or cut, respectively, for T_1, T_2 and T_3) because some animals did not graze, or only took a few bites from these swards. Bite mass from the sum of 'A + B' segments indicate that bite masses during grazing of compressed segments of T_1 and T_2 were higher than bite masses from the normal sward segments. The smaller bite mass of 'A+B' for T_3 reflects the smaller mass of bites taken from cut segments.

In summary, it appears that cattle preferred grazing normal swards to grazing compressed or cut swards (T_1 and T_2).

Table 5. Least squares means of selected sward variables after grazing and variables of grazing behavior of cattle offered the choice of normal and compressed swards (T_1), normal and cut swards (T_2), and compressed and cut (T_3) tall fescue swards during 1 hour grazing meals (Exp. II).

		- - - - - - Treatment - - - - - -			- - - - - - - - - Contrast - - - - - - - - -		
Variable	†Code A B	T_1 Normal Compressed	T_2 Normal Cut	T_3-- Compressed Cut	T_1 vs T_2	T1 vs T3	T_2 vs T_3
					- - - - - - - - Probability - - - --- -		
DM intake (kg)	A	1.28	1.49	1.11	0.29	0.40	0.06
	B	0.71	1.00	0.95	0.14	0.21	0.81
	A + B	1.99	2.49	2.06	0.07	0.80	0.12
DM utilization	A	0.33	0.37	0.29	0.40	0.41	0.10
	B	0.18	0.33	0.32	<0.01	<0.01	0.98
	A + B	0.25	0.35	0.31	<0.01	<0.01	0.09
Bites min^{-1}	A + B	28.1	30.6	28.6	0.15	0.75	0.26
Bite fraction	A/(A+B)	0.74	0.79	0.50	0.64	0.02	<0.01
Bite DM mass (g)	A + B	1.24	1.36	1.23	0.36	0.95	0.33

They grazed equally on compressed and cut sward segments when given the opportunity (T_3). Compressed swards supported larger bite masses than normal swards and cut swards. Cattle ingested more total herbage from normal and cut swards (T_2) than other sward treatments (T_2 and T_3).

Discussion

Herbage Intake from Normal and Compressed Swards

Compression of vegetative grass swards by weighted plywood overnight lowered sward surfaces from 34 to 14 cm and resulted in a 3-fold increase in sward dry matter (DM) density. In our opinion, sward compression simulated lodging. Sward compression did not alter linear and mass dimensions of the vegetative tillers, nor did it alter the herbage DM mass of herbage DM allowance. In compressed swards, leaf blades, which reached 39 cm when extended, were layered in narrow horizons of about 5 cm depth located above the pseudostem horizon, which was about 9 cm above the soil surface. Arias et al. (1990) suggested that pseudostems of tall fescue swards form a mechanical barrier to prehension biting and restrict grazing to herbage above 9–11 cm. The leaf arrangement of compressed swards was quite different from the apparently random arrangement of blades of unaltered swards where leaf angles vary widely and where fully extended blades are flagged. Thus, cattle offered compressed swards were exposed to higher sward DM densities, lower sward surface heights, and altered canopy architecture. All of these factors moderate grazing behavior (Hodgson et al. 1994).

Analysis of variance did not detect significant linear trends in herbage intake over successive days, thus we can assume that compression did not affect acceptance of normal or compressed swards and, further, that our cattle did not need to learn to graze them (Provenza and Balch 1987). It can be assumed that our cattle had been exposed to lodged swards because tall fescue pastures in Kentucky are partly or wholly lodged by the wind and the wind-driven rains that accompany thunderstorms. Each year about 50 thunderstorms are recorded at locations in the Central Bluegrass Region of Kentucky and there are about 30 days each year with more than 25 mm of rain (Priddy 1993).

The dry matter (DM) intake rate was about 10% higher for cattle grazing compressed swards (T_2) than for cattle grazing normal swards (T_1). This small increase is surprising, considering that sward surfaces were lowered by more than 40% and that DM density of swards increased more than 3-fold. Higher DM intake rates of cattle grazing compressed swards were largely attributable to larger bite mass. Compressed (T_2) and split (T_3) swards resulted in mean bite DM masses that were 127 and 141% heavier, respectively, than of bites of cattle grazing normal swards (T_1).

The relatively small increase in bite mass in response to a three-fold increase in sward DM density was associated with a decline in estimated mean bite volume from 1.45 liters (T_1) to 0.56 liters (T_2) and 0.47 liters (T_3). We suggest that bite depth, an important component of bite volume (Hodgson et al. 1994), was limited to a sward horizon of about 5 cm in depth, delimited by a plane fixed by the top of pseudostems (Arias et al. 1990). If 0.56 liters of sward (T_2) were prehended as a 5 cm tall cylinder then the bite diameter would be about 19 cm. For animals grazing the normal sward (T_1) with a bite depth of 18 cm and a bite volume of 1.45 liters, bite diameter would be about 10 cm. Thus, we conclude that sward compression forced animals to take shallow bites with a wider bite area. Typically, bite depth of grazing animals is largely determined by sward properties (Laca et al. 1992), whereas bite areas are largely determined by the herbage gathering capacity of the tongue and mouth (Illius and Gordon 1987). It appears that bite mass did not fully reflect the higher DM densities of lodged swards because cattle had limited capacity to modulate bite area.

Preference of Cattle for Normal or Compressed Swards

When our grazing cattle were given a choice, over 60% of ingested herbage dry matter (DM) came from normal sward segments and the rest from compressed sward segments or cut sward segments. We concluded that this response was not related to difficulty in prehension of lodged herbage because, in Exp. I, cattle grazed compressed swards faster (0.31 kg 100 kg^{-1} $hour^{-1}$) than they grazed normal swards (0.27 kg 100 kg^{-1} $hour^{-1}$). Rates of biting of 28 and 25 bites min^{-1} for cattle grazing normal and compressed swards, respectively, do not indicate that compressed swards were difficult to graze. This small difference in rate of biting more likely reflects its negative relationship with bite mass because animals taking larger bite masses devote more jaw movements to mastication and bolus formation (Forbes 1988).

The preference of grazing cattle for normal swards over compressed swards may be simply related to differences in sward height. When offered both, they preferred normal to compressed or cut swards. When offered compressed or cut swards, however, they expressed a slight preference for compressed swards. In Exp. II, surfaces of normal swards were 27 cm above the soil surface while sward surfaces of compressed and cut swards were 16 and 20 cm, respectively. Griffiths et al. (1995) reported that their dairy cows offered the choice of 5 sward heights preferentially grazed the taller ones. They also reported that their grazing cattle did not respond to differences in bulk density of swards.

When one considers how cattle discriminated between normal and lodged swards, one concludes that the decision was probably made on the basis of vision (Illius and Gordon 1990). Field observations indicate that cattle, after entering small pastures, locate areas of taller herbage, apparently by sight, and then commence grazing. Such behavior would be prudent in the presence of predators (Newman et al. 1995). Apparently this selection process is not followed when the taller sward components are associated with dung deposits (Bao et al. 1998).

Other sensory means herbivores use in diet selection (Provenza and Balch 1987) did not appear to be involved in the decision making processes as the normal and lodged swards differed only in sward architecture. Evidently, they did not select swards because of higher energy density, as would be predicted by foraging theory (Stephens and Krebs 1986), nor did they attempt to maximize short term energy intake (Ungar et al. 1991, Distel et al. 1995). As normal and compressed swards were composed of similar plant material, one can assume that herbage quality characteristics were not involved in diet selection (Minson and Wilson 1994).

There was some indication that grazing was stimulated when cattle were offered normal/compressed swards and normal/cut swards. According to some reports, grazing activity may be briefly stimulated by exposure to new pastures (Dougherty et al. 1992, Forbes and Hodgson 1985), however, such aresponse is unlikely because of the briefness of grazing periods. Diet learning was probably not involved in the preference of animals for grazing normal swards over compressed swards because cattle had almost certainly been previously exposed to lodged swards in Kentucky grasslands.

Logic based on grazing down of pastures by horizon is a practical approach to modeling of grazing activity and is used in the GRAZE simulation model (Loewer 1998). Cattle graze tall grass swards down horizon by horizon until they encounter physical barriers to prehension, such as the pseudostems of tall fescue (Arias et al. 1990). Logic for advanced simulation models also requires behavior-based logic that accounts for spatial variability in herbage mass and sward surface height and patch selection (Distel et al. 1995). Our research indicates that lodging may alter patch selection in taller swards.

Knowing that grazing animals are able to maintain intake rates when grazing lodged swards may be of interest to grass breeders selecting grasses with low structural strength to facilitate intake and particle size reduction (Nguyen et al. 1982, Wright and Vincent 1996) because this trait will likely lead to increased lodging. In lodged swards, however, one can anticipate that lower crop growth rates, accelerated senescence, and declining herbage quality eventually reduce herbage intake (Minson and Wilson 1994).

Conclusions

Compression of swards is a satisfactory method of simulating short term lodging. Grazing behavior indicated that our animals were familiar with lodged swards and that they did not need to learn to graze them. Further, our cattle grazed lodged swards at slightly faster rates of intake than they grazed normal swards because they were able to compensate for lower bite depth by increasing bite area, and because the higher sward dry matter (DM) densities resulted in increased bite mass. When offered a choice, our cattle preferred grazing normal swards to lodged or defoliated swards, probably because of greater sward surface height or sward bulk. We suggest that vision was involved in the decision making process and that sight played an important role in spatial diet selection. Our data also supports simulation logic that assumes that large generalist herbivores graze pastures down, horizon by horizon.

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J. Range Manage.
52:515–518 September 1999

Deer damage to alfalfa and mixtures with timothy or orchardgrass

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Abstract

White-tailed deer (*Odocoileus virginianus* L.) feed heavily on alfalfa (*Medicago sativa* L.) throughout Pennsylvania. Attempts to reduce deer feeding on forage crops have proven too costly or ineffective. The objective of this research was to determine the loss in yield and economic returns caused by deer feeding on pure and mixed stands of perennial forage crops. At 2 locations in central Pennsylvania, plots of pure alfalfa, timothy, and orchardgrass, and alfalfa-grass mixtures of 25, 50, and 75% alfalfa were established within areas protected (with fencing) or unprotected from deer. Forage was harvested and dry matter yields, percentage of alfalfa and grass, forage quality, and net economic returns were determined. Deer reduced forage dry matter (DM) yield by 1,451 kg ha^{-1} yr^{-1}. Deer feeding also reduced annual yield of pure alfalfa by an average of 54%, while yields of pure orchardgrass were reduced by only 7%, resulting in average economic losses of \$198 and \$59 ha^{-1} for pure alfalfa and pure orchardgrass, respectively. Deer fed more on plots containing timothy than those containing orchardgrass. Forage quality was unaffected by deer feeding but declined as the proportion of alfalfa to grass in the mixture declined. In unprotected areas, mixtures seeded at 50% timothy or 25 to 75% orchardgrass produced greater economic returns than pure alfalfa.

Key Words: white-tailed deer, economics

Resumen

En Pennsilvania, el venado cola blanca (*Odocoileus virginianus* L.) se alimenta en gran parte de "Alfalfa" (*Medicaco sativa* L.). Los intentos para reducir que los venados se alimenten de cultivos forrajeros han sido costosos e inefectivos. El objetivo de este estudio fue determinar las perdidas en rendimiento y retorno económico causado por la alimentación de los venados en poblaciones puras y mezcladas de cultivos forrajeros perennes. El estudio se condujo en 2 localidades de la parte central de Pennsilvania. Se establecieron parcelas de "Alfalfa", "Timothy" y "Orchardgrass" puros y parcelas de "Alfalfa" mezclada con un 25, 50 y 75% de zacate. Se establecieron 2 grupos de parcelas, unas protegidas (cercadas) contra el venado y otras sin protección. Las parcelas se cosecharon y se determinó el rendimiento de materia seca, porcentaje de "Alfalfa" y zacate, calidad de forraje y el retorno neto económico. El venado redujo en 1,451 kg ha^{-1} año^{-1} el rendimiento anual de materia seca de forraje. La alimentación del venado también redujo en 54% el rendimiento anual de la "Alfalfa " pura, mientras que el rendimiento del "Orchardgrass" puro se redujo solo un 7%. En promedio, las perdidas económicas fueron del orden de \$198 y \$ 59 dólares ha^{-1} para "Alfalfa" pura y "Orchardgrass" puro respectivamente. El venado se alimento más en parcelas que contenían "Timothy" que en las que contenían "Orchardgrass". La calidad del forraje no fue afectada por la alimentación del venado, pero declino conforme la proporción de "Alfalfa" en la mezcla disminyo. En áreas sin protección las mezclas sembradas con 50% de "Timothy" o 25 a 50 % de "Orchardgrass" produjeron mayores retornos económicos que la "Alfalfa" pura.

Due to its relatively high nutritional value, alfalfa is a major component of dairy and livestock diets in Pennsylvania (Penn. Ag. Stats. Service 1997). However, white-tailed deer, which are native to Pennsylvania's woodlands, have adapted well to living among Pennsylvania's farmland and can cause considerable damage to alfalfa (English and Bramble 1949, Kosack 1996, Schumacher 1997, Shope 1970). Thomas (1954) reported that deer caused a 78% yield reduction in alfalfa fields. Palmer et al. (1982) reported yield losses of 20% and economic losses of \$209 ha^{-1} when deer fed in Pennsylvania alfalfa fields.

Various types of deterrents (e.g. fencing, spreading repellents such as fecal matter and urine of natural deer predators, and installing noise making devices in and around fields) have been used in an attempt to prevent deer damage to crops. These attempts have been unsatisfactory because of high costs, ineffectiveness, or both (George et al. 1983, Andelt et al. 1991, Vecellio et al. 1994).

In a New Zealand study, deer preferred legumes over grasses (Hunt and Hay 1989). English and Bramble (1949), in a Pennsylvania study, reported that deer "are none discriminating except in choosing the best forage available". Also in Pennsylvania, Thomas (1954) observed that "...the deer would graze fields selectively by nipping the tops out of the clover and alfalfa plants, leaving the grasses unharmed." Thomas also noted that deer damage to pure legume hay was heavier than damage done to legume-grass mixed hay. Use of alternative forage species or forage mixtures to minimize deer feeding and economic loss is warranted.

Manuscript accepted 14 Dec. 1998.

Failures in attempts to control deer feeding on alfalfa and reports that deer prefer legumes over grasses, prompted this research to test an agronomic solution to deer damage to forage crops. The objective of this research was to determine yield and economic losses associated with deer feeding on pure and mixed stands of perennial forage crops.

Forages were seeded during August 1994 into a Buchanan channery loam (fine-loamy, mixed, mexic Aquic Fraguidult) soil at 2 sites on the Russell E. Larson Agricultural Research Center near Rocksprings, Penn. (40°48'N, 77°52'W, Elev. 372 m). Both sites, near wooded mountain ridges, were bordered by corn or alfalfa. Lime and soil nutrients were applied prior to seeding according to soil test recommendations to achieve optimum levels.

'Pioneer 5373' alfalfa, 'Toro' timothy (*Pleum pratense* L.), and 'Pennlate' orchardgrass (*Dactylis glomerata* L.) were seeded into 2 by 6.1 m plots to achieve pure stands of each species and mixed stands of 25, 50, and 75% alfalfa. Seeding mixtures were replicated 4 times in a split-plot arrangement of a randomized complete block design. Whole plots were contained within "deer proof" fence or left unfenced and accessible to deer for grazing. The deer-proof fence consisted of 3 strands of electrified super-wide, positive-negative hot tape (Premier, Washington, Iowa) at 30, 80, and 135 cm heights charged with 6300 volts.

Plots were mechanically harvested in 1995 and 1996 when the alfalfa was in the early flower stage (Kalu and Fick 1981). Prior to mechanical harvesting, visual estimates of forage persistence were made and a hand-harvested sample was collected from a randomly selected 0.3 m strip across each plot to determine percent species composition. Approximately 1 kg of the mechanically harvested forage from each plot was oven dried at 60°C for 48 hours for dry matter (DM) determination and then ground to pass a 1 mm screen for quality analysis.

Quality analyses included crude protein content (CP, Kjeldahl N x 6.25), acid detergent fiber (ADF), and neutral detergent fiber (NDF) (Goering and Van Soest 1970) using Near-Infrared Reflectance Spectroscopy (NIRS). In 1995, 80 samples were selected from all harvested samples using the SELECT program described by Shenk and Westerhaus (1994) and analyzed chemically for CP, ADF, and NDF. These 80 samples were used to create a calibration equation to predict constituents of all samples collected in 1995. In 1996, 40 samples were selected using the SELECT program, chemically analyzed, and added to the NIRS prediction equation from 1995 to predict the quality of samples collected in 1996.

After each harvest, 33.6 kg ha^{-1} N (ammonium nitrate) was applied to all plots. To control potato leafhopper (*Empoasca fabae* Harris), Dimethoate (0,0-dimethyl S-[N-methylcarbamoyl)-methyl] phosphorodiathioate) insecticide was used as needed.

Economic comparison between treatments was based on the difference between the value of harvested forage and variable costs of production. Forage value was based on CP, and TDN (total digestible nutrients) content and yield relative to a reference forage with CP, TDN, and $/Mg (metric ton) values of 16%, 54%, and $93.50 respectively (Hall and Eckert 1992, Linn and Martin 1985). Cash values were established at which the forage nutrients above the reference forage level could be obtained by purchasing corn (*Zea mays* L.) grain and soybean (*Glycine max* L.) meal for sources of TDN and CP, respectively. Corn and soybean meal were priced at $0.11 kg^{-1} and $0.29 kg^{-1}, respectively.

Variable costs of production were detected from revenue generated by each treatment to determine net economic return. Harvest costs were assessed at $69 ha^{-1} per harvest (Hall and Marshall 1996) and fertilizer and insecticide costs were set at $37 and $23.50 ha^{-1} per application, respectively. Nitrogen and insecticide costs were not added to production costs for treatments with more than and less than 50% alfalfa, respectively, as these treatments would not normally receive nitrogen or insecticide.

Data from each location were analyzed initially as a split-plot arrangement of a randomized complete block design. The homogeneity of variance was tested and data were than analyzed over locations and years. Least significant difference values (0.05) were calculated for statistical comparisons among treatments.

Results and Discussion

Growth Environment

In 1995 and 1996, precipitation was below and near normal, respectively. Although no method was used to definitively determine deer grazing pressure on the research sites, it was believed to be typical of grazing pressure throughout much of Pennsylvania. At times, as many as 7 deer were observed grazing the unprotected research area (about 0.08 ha).

Forage Yield:

Averaged over all unprotected treatments, deer consumed 1,451 kg of forages ha^{-1} (Fig. 1). Deer feeding reduced total yield of pure alfalfa treatments by 54% while total yields of pure orchardgrass treatments were reduced by only 7%. Pure orchardgrass produced the greatest forage yield among unprotected plots. These yield reductions are greater than those previously reported by Palmer et al. (1982) but less than those reported by Thomas (1954). In the unprotected areas, all seeding mixtures and pure grass produced greater yields than pure alfalfa.

Deer selectivity grazed alfalfa out of the alfalfa-grass mixtures. Averaged over all protected plots, alfalfa constituted 35% of the total yield but in unprotected plots, alfalfa constituted only 19% of the total yield. This finding supports previous observations by Thomas (1954), and Hunt and Hay (1989) that deer prefer legumes over grasses in mixed stands.

Deer fed more in plots that contained timothy than those containing orchardgrass. Averaged over all unprotected plots containing timothy and orchardgrass, yields averaged 35 and 20% less, respectively, than their protected counterparts. This indicates that, in this study as in Thomas's (1954) work, timothy was more palatable to deer than orchardgrass.

Forage Persistence and Weed Yield:

Deer feeding resulted in lower forage persistence and an average of 1,199 kg ha^{-1} greater weed yield than in protected plots during the second year of the study (data not shown). Weed yields were greatest in the pure alfalfa plots and

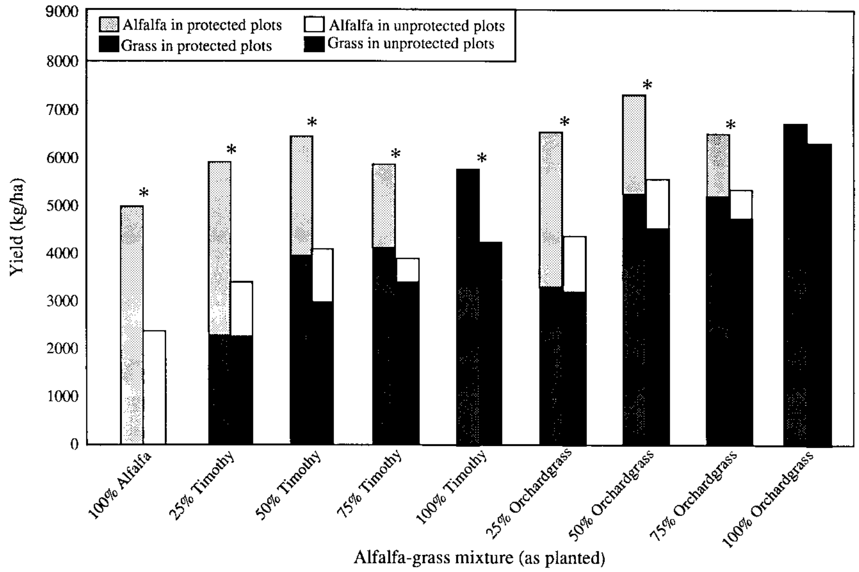

Fig. 1. Dry matter yield from pure stands and mixtures of alfalfa and timothy or orchardgrass that were protected or unprotected from deer feeding. Values are the mean of 2 locations over 2 years. Protected or unprotected means of total yield with an * are different at the 0.05 level.

decreased as the amount of grass in the seeding mixture increased. The lowest weed yields were in the pure orchardgrass plots. Weed yields in the second year of the study were directly related (R^2=0.64; y=86+2.15X) to the reduction in forage yield caused by deer feeding in the first year. Unfortunately, alfalfa in all treatments was winterkilled before the 1997-growing season leaving the long-term effect of deer feeding on stand persistence undocumented.

Forage Quality:

In general, CP, ADF, and NDF content of the forage were not affected by deer feeding (data not shown). This was unexpected considering the selective grazing of alfalfa from the unprotected plots. However, the relatively frequent harvest schedule used in this research probably minimized differences in quality that may have been observed with less frequent harvests (i.e. more mature forages). Over all treatments, forage quality between seeding treatments was pure alfalfa>alfalfa-timothy mixtures>alfalfa-orchardgrass mixtures.

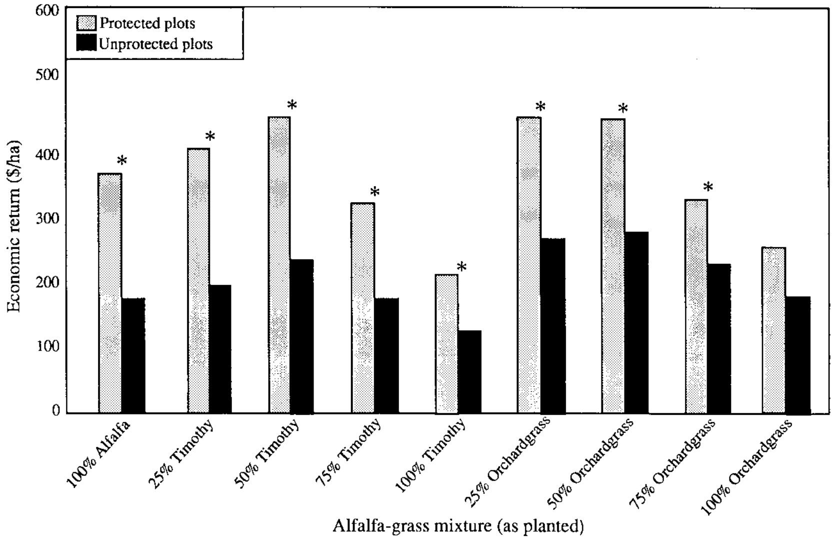

Fig. 2. Economic return from pure stands and mixtures of forages that were protected or unprotected from deer feeding. Values are the mean of 2 locations over 2 years. Protected or unprotected means with an * are different at the 0.05 level.

Net Return:

Deer feeding on forages resulted in average economic losses of $152 ha $^{-1}$ (Fig. 2). The economic impact associated with deer feeding in this study was similar to those reported by Palmer et al. (1982). Averaged over all unprotected treatments, mixtures containing orchardgrass had $59 ha^{-1} greater economic returns than mixtures containing timothy. This result is in direct response to the increased deer feeding on timothy mixtures. Under situations where deer had access to forage crops, seeding mixtures of alfalfa with 50% timothy or 25 to 75% orchardgrass gave the greatest economic returns. The apparent discrepancy between high forage yield and low economic returns with pure orchardgrass is due to its lower forage quality and lower forage value relative to other treatments.

Conclusions

Deer feeding caused significant yield and economic losses to alfalfa and alfalfa-grass mixtures. Deer selectively grazed alfalfa out of alfalfa-grass mixtures and preferred timothy over orchardgrass. Orchardgrass alone or seeded in mixture at greater than 50% minimized deer feeding and resulted in the greatest forage yields. However, greatest economic return resulted with seeding mixtures containing 50% timothy or 25 to 75% orchardgrass.

The results of this research indicate that farmers who experience deer damage to their alfalfa and can not exclude the deer with fencing may be able to minimize the negative effect of deer feeding by seeding alfalfa-grass mixtures. Dairy farmers who can realize increased income (milk production) from high quality forages should consider seeding alfalfa mixed with 50% timothy or 25 to 50% orchardgrass. These treatments produced maximum economic returns based on yield and forage quality. On the other-hand, farmers with livestock that do not require high quality forage (e.g. brood cows) should plant pure orchardgrass for maximum forage yield.

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J. Range Manage.
52:519–524 September 1999

Diversity of the herbaceous layer in mixed bushveld

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Abstract

The diversity of the herbaceous layer in the Nylsvley Nature Reserve (Mixed Bushveld) was investigated to enhance the understanding of savanna ecosystems and to serve as a baseline for future monitoring to facilitate management. Species composition and density, dry weight contribution per species, and grass density was measured with a small-quadrat method. A total of 73 grass species were recorded. Plant communities were compared in terms of percentage composition and percentage dry weight per ecological group, species diversity and grass density with general linear modeling. The herbaceous layer of most plant communities consisted predominantly of increaser I species (increasing in under-utilized areas), with increaser I and decreaser species (decreasing with under or over-utilization) producing the highest biomass. The dominance of increaser III species (becoming dominant in heavily over-grazed areas) in the *Sporobolus ioclados -Acacia tortilis* Savanna indicates previous over-utilization of this plant community. A generally high species diversity (Simpson's index 1-D >0.72) in the reserve is influenced by environmental factors and is a reflection of previous low animal stocking densities and a rotational burning regime. Grass density varied from 53.07 to 219.13 grasses/m^{-2}. A negative correlation (r = –0.6654) between grass density and species density supports the principle that species diversity is reduced in over-grazed areas. The high diversity of the herbaceous layer in the Nylsvley Nature Reserve may serve as a benchmark for comparing range diversity over time and space within this vegetation type.

Key Words: species composition, species density, species diversity, percentage dry weight, grass density, Simpson's index, bootstrapping

Resumen

Se investigó la diversidad del estrato herbáceo en la Reserva Natural Nylsvley (Mixed Bushveld) para aumentar el entendimiento de los ecosistemas de savana , que sirva de referencia para futuras comparaciones y facilitar el manejo. La composición y densidad de las especies, la contribución del peso seco por especie y la densidad de pasto fueron medidas con el método del cuadrante pequeño. Se registraron un total de 73 especies de pastos. Las comunidades de plantas se compararon en términos de porcentaje de composición y peso seco por grupo ecológico, diversidad de especies y densidad de pastos la comparacion se hizó mediante modelos lineales generales. El estrato herbáceo de la mayoría de las comunidades de plantas consistió principalmente de especies incresoras I (que aumentan en áreas subutilizadas), las especies incresoras I y decresoras (que disminuyen con sub o sobreutilización) produjeron la mayor cantidad de biomasa. La dominancia de especies incresoras III (dominantes en áreas fuertemente sobreutlizadas) en la savana de *Isporobolus iocladosy-Acacia tortilis* indican una sobreutilización previa de esta comunidad. La alta diversidad de especies (Indice de Simpson 1-D>0.72) de la reserva esta influenciada por factores ambientales y también es un reflejo de la baja densidad de carga animal anterior y un régimen rotacional de quemas. La densidad de pasto vario de 53.07 a 219.13 pastos m^{-2}. Una correlación negativa (r = –0.6654) entre los pastos y la densidad de especies refuerza el principio de que la diversidad de especies es reducida en áreas sobreutilizadas. La alta diversidad del estrato herbáceo en la reserva natural de Nylsvley puede servir como una referencia para comparar el rango de diversidad a través del tiempo y el espacio dentro de este tipo de vegetación.

The herbaceous layer composition is changing continuously in space and time due to a combination of factors, such as grazing, fire, and rainfall which differ in intensity, duration, and timing. O'Connor (1991) found that rainfall variability over 1 or 2 years could induce substantial changes in composition. Composition is further affected by grazing. Tuft survival of grass species decreased by approximately 48 % under rainfall interception and grazing experiments (O'Connor 1991). The high species diversity in the Nylsvley Nature Reserve is attributable to the diversity of habitats, the climatic, geomorphological and biogeographical history of the region, and the long period of uninterrupted, evolutionary development (Scholes and Walker 1993).

When only a sample of species in the community is obtained, it is necessary to distinguish between numerical species richness, that is number of species per specified number of individuals or biomass, and species density, that is number of species per specified collection area (Magurran 1991). Species evenness or equitability refers to how equally abundances (number of individuals, biomass and cover) are distributed among species (Goldsmith et al. 1986, Ludwig and

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Research was funded by the Foundation for Research Development and partly by Technikon SA. Environmental Affairs Northern Province gave permission to conduct the study in the Nylsvley Nature Reserves.

Manuscript accepted 29 Nov. 1998.

Reynolds 1988, Morrison et al. 1992). Diversity indices combine both species richness and evenness into a single value (Ludwig and Reynolds 1988, Magurran 1991) and are therefore more suitable for analysis of community structure. These are also called heterogeneity indices (Ludwig and Reynolds 1988). The advantage of diversity indices is that no assumptions about distribution of individuals among species have to be made (Morrison et al. 1992), and they are therefore referred to as non-parametric indices (Magurran 1991). Although the greatest problem with diversity indices is interpretation of their values, they are widely applied in community analyses (Ludwig and Reynolds 1988, Magurran 1991, Morrison et al. 1992). These indices merely reflect community structure by changing with species richness, equitability and sometimes density (Morrison et al. 1992). Simpson's index (D) is commonly used (Magurran 1991) and is based on probability theory (Goldsmith et al. 1986). It measures the probability that 2 individuals selected at random from a sample belong to different species. Simpson's index is most sensitive to changes in common species (Magurran 1991, Morrison et al. 1992). Abundance or density of grasses is defined as number of individuals of a particular species per unit area (Goldsmith et al. 1986, Causton 1988, Goldsmith 1991) which is related to biomass. For the same height, grass quantity varies according to the density (Voisin 1988).

In the late 1970s and 1980s alpha diversity (number of species in a defined area) was measured only in the *Eragrostis pallens–Burkea africana* savanna as part of the Savanna Biome Programme. An alpha diversity of 319 plant species was high by global standards of 80 to 100 species 0.1 ha^{-1}. Disturbed areas with fertile soils within this plant community had a diversity of 40 to 60 species 0.1 ha^{-1} (Scholes and Walker 1993). However no work has been published on the herbaceous diversity of the entire Nylsvley Nature Reserve. A more in-depth knowledge of the diversity of the herbaceous layer can serve as a benchmark for future monitoring which would facilitate management. Objectives of this study were to estimate and compare percentage composition and percentage dry weight per ecological group, species density and diversity and grass density between plant communities.

Materials and Methods

The study was conducted in the Nylsvley Nature Reserve (24°39'S 28°42'E), South Africa, situated in Mixed Bushveld on the border between a moist and dry savanna (Acocks 1988). The rainy season in summer (maximum mean daily temperature of 29.3°C) is followed by dry, cold winters (minimum mean daily temperature of 6.1°C). In the 1993/1994 and 1994/1995 rainy seasons, a rainfall of 480.5 mm and 512.4 mm, respectively was lower than the long-term rainfall of 623 mm (standard deviation of 134 mm) (Scholes and Walker 1993). Vegetation surveys were conducted in 8 plant communities, identified from a vegetation map constructed by Coetzee et al. (1976), Frost (1987), and Scholes and Walker (1993):

1. *Rhus leptodictya-Combretum apiculatum* Variation (lithosols underlain by rock)
2. *Cymbopogon plurinodis-Combretum apiculatum* Variation (lithosols underlain by rock)
3. *Eragrostis nindensis-Digitaria monodactyla* Variation (lithosols underlain by rock)
4. *Sporobolus ioclados-Acacia tortilis* Savanna (fine-textured illuvial soils with high clay contents)
5. Nyl River and floodplain (alluvial soils)
6. *Aristida bipartita-Setaria sphacelata* Savanna variation (vertisols and mollisols)
7. *Aristida bipartita-Setaria sphacelata* Grassland variation (vertisols and mollisols)
8. *Eragrostis pallens-Burkea africana* Savanna (well-drained, residual sandy soils)

Sampling

Snyman et al. (1990) suggested the dry-weight rank method, a small-quadrat method, and the comparative yield method to estimate herbaceous composition and phytomass, respectively of the semi-arid savanna of the Northern Province. In each plant community 3 sites were surveyed in February/March 1995. A stratified, non-random sampling approach was followed where, at each site, 20 quadrats (0.25 m^2) were placed 5 m apart on a single line transect (Dörgeloh 1997), assuming independence between sampling points.

Grass density

Each rooted herbaceous plant within a 0.25 m^2 square was counted. Density estimates were based on a convenient morphological unit. In this case each rooted aerial shoot was treated as a unit. It is almost impossible to determine the density of grass species which spread vegetatively (Goldsmith et al. 1986). Therefore rooted nodes of stolons of rhizomatic grasses and parts of tufts, that had split and were at least 2 centimetres from the nearest other plant of the same species, were counted as individuals. This was applied to all monocarpic (annuals and biennials) and polycarpic (perennials) species which usually have extensive below ground vegetative growth systems (Causton 1988).

Species composition and density

Each rooted grass species within a 0.25 m^2 square was identified according to Gibbs Russell et al. (1991) and Van Oudtshoorn (1992). Forbs as a group (≈15 species) was treated as a single species. Species density is the most commonly used measure of species richness (number of species) (Magurran 1991) and was calculated from the number of species per 15 m^2 for each plant community.

Biomass contribution per species

The relative biomass contribution of grass species was estimated with the dry-weight rank method, as developed by 't Mannetje and Haydock (1963) and described by Kelly and McNeill (1980), Barnes et al. (1982), Ben-Shahar (1991) and Shackleton (1992). Each of the 3 most dominant grass species or forb in a square was ranked according to its relative biomass contribution.

Data analysis

The hypotheses tested were that no differences existed between plant communities in terms of percentage composition and percentage dry weight per ecological group, species diversity, and grass density. Grass species were grouped into 4 ecological groups based on their response to grazing as described by Tainton (1984), Holechek et al. (1989), Snyman et al. (1990) and Van Oudtshoorn (1992). These were decreasers, that is species decreasing with over or under-utilization, increaser I, species increasing in under-utilized areas, and increaser II and increaser III species becoming dominant in moderate and heavily over-grazed areas, respectively. Species were grouped into ecological groups as described above.

Herbage mass of each ranked species was calculated using the multipliers proposed by ‘t Mannetje and Haydock (1963). Barnes et al. (1982) derived their own multipliers but these did not increase the precision of estimates significantly. They therefore recommended the use of multipliers of ‘t Mannetje and Haydock (1963).

Data of 3 sites was pooled for each plant community as suggested by Wratten and Fry (1980). Species diversity was calculated with Simpson’s index (D) using absolute species abundances. This index measures the probability that 2 individuals selected at random from a sample belong to different species. Therefore if the probability is high that both individuals belong to the same species, the diversity of the community is low. Because diversity decreases as D increases, Simpson’s index is usually expressed as 1-*D* (Magurran 1991). The equation of Simpson’s index described by (Wratten and Fry 1980, Goldsmith et al. 1986, Ludwig and Reynolds 1988, Magurran 1991, Morrison et al. 1992, Shukla and Srivastava 1992) is:

$$D = 1 - \sum\{[n_i(n_i - 1)]/[N(N - 1)]\} \quad \textbf{(1)}$$

where D = diversity index

n_i = number of individuals of species *i*

N = total number of individuals of all species in the sample

Simpson’s index value varies from 0 to 1. Low diversity (D = 0) occurs when each individual belongs to the same species and maximum diversity (D = 1) describes a community in which each individual belongs to a different species (Ludwig and Reynolds 1988).

Since an index gives only 1 value per area, it is not possible to test variation and statistical differences in species diversity among plant communities. To overcome this problem, bootstrapping or jacknifing techniques can be applied (Krebs 1989). These techniques are also used to estimate accuracy of ecological indices (Dixon 1993). The data set of each plant community was bootstrapped separately where 10,000 iterations, based on number and distribution of species, were selected randomly. A Simpson’s index value was calculated for each of these iterations. Paired tests of these data sets were then conducted between different combinations of plant communities. The bias of the bootstrap estimate of the mean was calculated as:

$$\text{Bias } (\overline{x}_S) = \overline{x}_B - \overline{x}_S \quad \textbf{(2)}$$

where $\overline{x}_B$ = bootstrap estimate of the mean

$\overline{x}_S$ = observed mean of the original sample (Krebs 1989)

Differences in percentage composition and percentage dry weight per ecological group, species diversity and grass density were tested with general linear modeling (SAS Inc. 1990) at a 95% confidence level.

Results

Percentage species composition and percentage dry weight per ecological group

Statistical analyses showed similarities among plant communities in terms of percentage species composition (p = 1.0) or percentage dry weight of ecological groups (p = 1.0). Most plant communities had a large percentage of increaser I grasses, with increaser I and decreaser grasses producing the largest dry weight (Table 1). Only *Sporobolus ioclados-Acacia tortilis* Savanna consisted predominantly of increaser III grasses in terms of percentage composition and percentage dry-weight (Table 1). The large percentage of increaser II in the *Eragrostis pallens-Burkea africana* Savanna was mainly the result of 1 species, *Digitaria eriantha* Steud. (Finger grass).

In terms of percentage composition and percentage dry weight *Setaria sphacelata* Schumach. (Common bristle grass) was dominant in plant communities on lithosols (1, 2, and 3). and *Sporobolus ioclados* Nees (Pan dropseed) in the *Sporobolus ioclados-Acacia tortilis* Savanna. In the Nyl floodplain *Leersia hexandra* Swartz (percentage composition) and *Panicum*

Table 1. Total percentage composition (%C) and percentage dry-weight (%DW) of each ecological group and plant community.

Plant community		DECR.	INC. I	INC. II	INC. III	STATUS UNKNOWN	FORBS
Rhus leptodictya -	% C	12.77	32.49	17.57	12.11		24.88
Combretum apiculatum Variation	% DW	13.79	36.70	41.03	7.22		2.29
Cymbopogon plurinodis -	% C	8.61	54.42	14.49	3.13		18.59
Combretum apiculatum Variation	% DW	11.22	70.26	9.74	4.88		3.97
Eragrostis nindensis-	% C	8.23	51.93	17.91	3.62		17.89
Digitaria monodactyla Variation	% DW	14.69	58.47	18.67	2.37		6.67
Sporobolus ioclados -	% C	1.22	0.00	21.20	45.81	1.19	30.57
Acacia tortilis Savanna	% DW	0.42	0.00	11.74	54.74	2.08	31.60
Nyl River and floodplain	% C	16.88	13.62	0.00	53.11		16.24
	% DW	77.37	13.06	0.00	17.51		8.96
Aristida bipartita- Setaria	% C	20.49	58.72	0.69	2.58	1.42	15.60
sphacelata Savanna Variation	% DW	48.67	40.87	0.42	3.60	4.27	1.66
Aristida bipartita-Setaria	% C	33.04	30.15	6.79	3.57	6.78	12.82
sphacelata Grassland Variation	% DW	71.80	11.73	5.21	0.17	0.00	12.09
Eragrostis pallens -	% C	19.48	1.38	51.65	5.65		21.86
Burkea africana Savanna	% DW	23.72	3.80	59.83	5.82		6.84

schinzii (percentage dry weight) were dominant. *Ischaemum afrum* Dandy (Turf grass) and *Themeda triandra* Forssk. (Red grass) were dominant in both *Aristida bipartita-Setaria sphacelata* plant communities (6 and 7) and *D. eriantha* (percentage composition) and *Eragrostis pallens* Hack. (Broom love grass) (percentage dry weight) in the *Eragrostis pallens- Burkea africana* Savanna. In most plant communities the large number of forbs had a low percentage dry weight (Table 1), except for *Sporobolus ioclados-Acacia tortilis* Savanna where it also had a large percentage dry weight.

Species density

A total of 73 grass species, including forbs as a group was recorded. Species density (species/15 m^2) was highest in plant communities on lithosols (1, 2, and 3) and lowest in the *Sporobolus ioclados-Acacia tortilis* Savanna and Nyl floodplain (Table 2).

Species diversity

Statistical tests of bootstrapped data based on species occurrence and eveness indicated no significant differences ($t < 1.96$) in species diversity among all plant communities. Species diversity of all plant communities was relatively high ($1\text{-}D > 0.72$) (Table 2). High index values of 3 plant communities on the lithosols (1, 2, and 3) indicate an even distribution of individuals among a large number of species. Fewer species and a less even distribution of abundances among species were found in the *Sporobolus ioclados-Acacia tortilis* Savanna and the *Aristida bipartita-Setaria sphacelata* Savanna Variation (Table 2).

Grass density

Grass density differed among plant communities ($p < 0.05$). The high grass densities in the *Sporobolus ioclados-Acacia tortilis* Savanna and the *Aristida bipartita-Setaria sphacelata* plant communities (6 and 7) (Table 2) differed significantly ($p < 0.05$) from one another and from plant communities on lithosols (1, 2, and 3). Grass densities in the Nyl floodplain differed from the *Sporobolus ioclados-Acacia tortilis* Savanna and those plant communities on the lithosols (1, 2, and 3). The *Eragrostis pallens-Burkea africana* Savanna did not differ ($p > 0.05$) from the latter plant communities. A negative correlation coefficient of $r = -0.6654$ was found between grass density and species density.

Discussion

Percentage composition and percentage dry weight per ecological group

The generally high biomass and percentage composition of decreaser 17.1% (SD 8.57) and increaser I species 34.7% (SD 21.77) indicate a low grazing pressure in the Nylsvley Nature Reserve. These figures exclude data from the over-grazed *Sporobolus ioclados-Acacia tortilis* Savanna. This is a reflection of maintaining low numbers of wild animals (≈0.29 animals ha^{-1}) on the reserve over 2 decades. In comparison Smit and Rethman (1992) recorded 6.8% decreasers and 18.3% increaser I species in long-term grazing trials (initiated in 1935/36) at low stocking densities of 0.25 animal units ha^{-1} and continuous grazing in Sourish Mixed Bushveld. This vegetation type is adjacent to Mixed Bushveld and has a similar climate. The grazing density of their trials may be comparable to the grazing regime in the Nylsvley Nature Reserve. Friedel (1988) recorded 8 % decreasers after 35 years of light grazing in *Combretum apiculatum* veld, and 41 % in *Acacia tortilis* veld protected from grazing in Mixed Bushveld.

The present degraded state of the *Sporobolus ioclados-Acacia tortilis* Savanna, dominated by increaser III grasses (45.8%) is due mainly to the historic over-utilization by cattle (> 20 years ago) (Scholes and Walker 1993) and the long-term concentration of game in this plant community (casual observation). The herbaceous layer of this plant community was also in poor condition (Dörgeloh 1999).

Species density and diversity

The relatively large species densities found in the Nylsvley Nature Reserve can be attributed to the diversity of habitats, the climatic, geomorphological, and biogeographical history of the region. A low stocking density maintained over

Table 2. Species density, species diversity and mean grass density (SE is given in brackets) per plant community.

Plant community	Species density	Simpson's index 1-D (SE - Bias)	Mean grass density
	(species/15 m^2)		(grasses/m^2)
Rhus leptodictya-Combretum apiculatum Variation	29	0.8362 (0.00045–0.0110)	71.0 (7.31)
Cymbopogon plurinodis-Combretum apiculatum Variation	27	0.8135 (0.00074–0.0473)	68.1 (4.78)
Eragrostis nindensis-Digitaria monodactyla Variation	25	0.8306 (0.00062–0.0362)	88.3 (3.68)
Sporobolus ioclados-Acacia tortilis Savanna	12	0.7273 (0.00093–0.0067)	219.1 (36.89)
Nyl River and floodplain	10	0.7921 (0.00054–0,0129)	135.1 (20.59)
Aristida bipartita-Setaria sphacelata Savanna Variation	21	0.7221 (0.00117–0.0832)	126.9 (11.53)
Aristida bipartita-Setaria sphacelata Grassland Variation	15	0.7917 (0.00066–0.0088)	147.8 (21.21)
Eragrostis pallens-Burkea africana Savanna	17	0.7725 (0.00071–0.0094)	53.1 (4.07)

many year s and a rotational burning regime may have resulted in the evenness of species and therefore similar species diversities among plant communities. Below average rainfalls of –18% in 1994/1995 and –23% in 1993/1994, although still within the long term average rainfall of 623 mm (standard deviation of 134 mm), did not affect the herbaceous diversity negatively.

Few studies have been conducted on the species composition in Mixed Bushveld (Lubke et al. 1983, Friedel 1988, Peel et al. 1991) or Sourish Mixed Bushveld (Smit and Rethman 1992). The methods used by these authors were mostly line transects which do not provide a measure of quantity (Friedel 1988). Lubke et al. (1983) estimated total plant diversity with a quadrat method only in the *Burkea africana-Eragrostis pallens* Savanna. Data on species composition was generally used to assess range condition rendering it difficult to compare species density and diversity, or grass density.

Grass density

Eragrostis lehmanniana Nees (Lehmann's lovegrass) was the principal contributor to the very high grass densities in the *Sporobolus ioclados-Acacia tortilis* Savanna. In the *Aristida bipartita -Setaria sphacelata* plant communities (6 and 7) *Cynodon dactylon* Pers. (Couch grass) and *I. afrum* contributed to the high grass densities. The stoloniferous growth forms of *dactylon* and *I. afrum* may have led to an over-estimation of grass density.

The negative correlation between grass density and species density showed that over-grazing as found in the *Sporobolus ioclados-Acacia tortilis* Savanna, may have reduced species diversity. Under these over-utilized conditions, species richness decreases with an accompanying increase in dominance of a few species adapted to high grazing pressures. The abundance of grass species becomes unevenly distributed (Morrison et al. 1992) and the system becomes more simple in terms of biodiversity.

Conclusion

The high diversity of the herbaceous layer in the Nylsvley Nature Reserve is influenced by climatic, geomorphological and biogeographical factors and is a reflection of previous low animal stocking densities (≈0.29 animals ha^{-1}) maintained over 2 decades. A long-term rotational burning programme where each plant community was burned at 2 to 3 year intervals probably also enhanced the herbaceous diversity. Slightly lower than average rainfalls did not affect the herbaceous diversity negatively. These results of the diversity of the herbaceous layer may serve as a benchmark for comparing range diversity over time and space within this vegetation type.

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Western juniper expansion on adjacent disturbed and near-relict sites

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Abstract

We determined rates of western juniper (*Juniperus occidentalis* spp. occidentalis Hook.) density and cover change during the period 1951 to 1994 at 3 adjacent sites with nearly identical elevation, slope, aspect, soils, plant communities, and climate, but different land-use histories. The 3 sites are located in central Oregon at the confluence of the Deschutes and Crooked Rivers. Two of the sites are typical of central Oregon rangelands in that they have a history of anthropogenic disturbance including active fire suppression and domestic livestock grazing. The third site is a relict mesa that is a protected Research Natural Area and has experienced minimal anthropogenic impacts. We used large scale aerial photography to determine cover and density of western juniper in 1951, 1956, 1961, 1972, 1982, and 1994. We found that western juniper density and cover during the last 4 decades increased at all sites, with changes on the relict site similar to those on one of the disturbed sites. We suggest that even though 2 of the traditionally cited causes of western juniper expansion since the late 1800s (altered fire regimes, domestic livestock grazing) may have contributed to expansion on our disturbed sites, these mechanisms can not explain expansion on the near-relict mesa. Further, we examined climatic changes since 1900 in the region and concluded that the data did not fully support a climate-driven mechanism for the expansion. In seeking to explain western juniper expansion on semiarid rangelands, we suggest that all potential causal mechanisms (e.g., fire history, biological inertia, climate, domestic grazing, atmospheric CO_2 enrichment) be considered.

Key Words: afforestation, central Oregon, land-use history, biological inertia

Resumen

Determinamos las tasas de densidad y cambio de cobertura del "Western Juniper" (*Juniperus occidentalis* spp. Occidentalis Hook.) ocurridas durante el período de 1951 a 1994 en 3 sitios adyacentes con elevación, pendiente, aspecto, suelos, comunidades vegetales y clíma casi idénticos pero con diferentes historias de uso de la tierra. Los 3 sitios se localizan en la parte central de Oregon en la convergencia de los ríos "Deschutes" y "Crooked". Dos de los sitios son típicos de los pastizales centrales de Oregon, los cuales tienen una historia de disturbio antropogénico incluyendo la supresión activa de fuego y el apacentamiento de ganado. El tercer sitio es un área natural reliquia protegida y para fines de investigación, y que ha experimentado impactos antropogénicos mínimos. Utilizamos fotografía aérea a gran escala para determinar la cobertura y densidad del "Western Juniper" en 1951, 1956, 1961, 1972, 1982 y 1994. Encontramos que en las últimas 4 décadas la densidad y cobertura del "Western Juniper" ha incrementado en todos los sitios, presentando el área reliquia cambios similares a los ocurridos en uno de los sitios con disturbio. Sugerimos que a pesar de que las 2 causas (supresión de fuego y apacentamiento de ganado domestico) tradicionalmente citadas como responsables de la expansión del "Western Juniper" ocurrida desde finales del siglo pasado pueden haber contribuido a la expansión en los dos sitios con disturbio; sin embargo, estos mecanismos no pueden explicar la expansión ocurrida en el área reliquia. Además, examinamos los cambios climáticos ocurridos en la región desde 1900 y concluimos que los datos no sustentan por completo una expansión inducida por el clíma. Sugerimos que en la búsqueda de la explicación de la expansión del "Western Juniper" en los pastizales semiáridos, se deben consider todos los mecanismos causales potenciales (por ejemplo, historia de fuego, inercia biológica, clíma, apacentamiento de ganado doméstico, incremento del CO_2 atmosférico).

Western juniper (*Juniperus occidentalis* spp. occidentalis Hook.) is the dominant tree of arid and semiarid Pacific Northwest woodlands (Agee 1993). Found in California, Idaho, Nevada, Oregon, Washington, it has undergone substantial afforestation during the last century, including increases in density and cover on previously occupied sites, and an approximate doubling of its range (Caraher 1978, Miller et al. 1987, Bedell et al. 1993). While older stands of western juniper are largely found on areas with “deep pumice sands”, “rock outcrops,” and “shallow soils underlain by deeply fractured bedrock,” the new woodlands are expanding into areas previously dominated by shrubs (e.g., *Artemesia tridentata* Nutt.-big sagebrush) and grasses (e.g., *Festuca idahoensis* Elmer.-Idaho fescue, *Agropyron spicatum* (Pursh) Scribn. & Sm.-bluebunch wheatgrass) (Bedell et al. 1993:4). There is concern that the rapid rate of expansion may result in western juniper super dominance in communities previously

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Manuscript accepted 20 Oct. 1998.

dominated by big sagebrush (Liverman 1993), and that juniper expansion may alter ecocsystem functioning via changes in species composition (e.g., Burkhardt and Tisdale 1969, Vaitkus and Eddleman 1991) and altered fire regimes (e.g., Burkhardt and Tisdale 1976, Agee 1993). It has been argued that these ecosystem alterations may result in the loss of wildlife habitat, reduced range productivity and diversity, and watershed degradation (Bedell et al. 1993, Liverman 1993). Others (e.g., Gifford 1987, Belsky 1996), however, have shown that some of the negative characteristics often associated with its expansion on the western range (e.g., decreased water infiltration, increased soil erosion, stream flow reduction, decreased wildlife habitat) are not fully supported.

Despite the uncertainty surrounding the ultimate consequences of western juniper expansion, it remains an issue with both ecological and management implications. Both the Oregon Department of Fish and Wildlife (ODFW) and the Bureau of Land Management (BLM) are interested in western juniper woodland management programs. Management projects proposed by the BLM would be extensive and expensive ($27,000,000+), involving selective cutting and prescribed burns on some 273,000+ ha of established and emerging juniper woodlands (Liverman 1993).

Dendrochronological studies have shown that historic western juniper expansion began in the late 1800s, and in the absence of reestablishment in sites of wood cutting the expansion has been chiefly linked with 3 causes: 1) reduction in fire frequency caused by organized fire suppression and/or by a reduction in fine fuels in areas of heavy livestock grazing; 2) the indirect effects of livestock grazing (e.g., fuel reduction and an increase in shrubby nurse plants); and 3) favorable climatic conditions (i.e., mild wet winters and cool wet springs) (Burkhardt and Tisdale 1976, Young and Evans 1981, Eddleman 1987, Miller and Rose 1995). However, none of the traditional explanations appear to be "entirely satisfactory in explaining" historic western juniper expansion (Young and Evans 1981:505). There is continued interest in examining the rates and probable causes of western juniper afforestation because: 1) the current expansion is occurring at geometric rates at some locales (Liverman 1993, Miller and Rose 1995), and 2) the causes of the current expansion are uncertain.

A rare opportunity to compare the effects of land-use history on western juniper expansion exists in central Oregon. At the confluence of the Deschutes and Crooked Rivers lie 3 sites of nearly identical elevation, slope, aspect, soils, plant communities and climate (Fig. 1). This geographical setting allows for minimizing the biotic and abiotic differences between sites that in turn provides for a more direct comparison of the effects of past land-use history. Further, large-scale aerial photography of all 3 sites exists from 1951 through 1994. Thus, the purpose of this paper is to: 1) document rates of western juniper expansion (i.e., density and cover increases) during the last 4 decades, and 2) address how land-use histories may have affected western juniper expansion on the 3 sites.

Study Site Characteristics

The Island Research Natural Area (IRNA) is a near-relict area managed by the Prineville District of the Bureau of Land Management (BLM), the Crooked River National Grasslands (part of the Ochoco National Forest), and Oregon State Parks. Because of its classification as a Research Natural Area, anthropogenic disturbances at IRNA are limited. Grazing is not allowed, fire suppression is not active, and the plateau is controlled by Oregon State Parks personnel with usage limited to scientific and educational activities. The area has not been grazed for over 70 years, and the only historical account of livestock grazing was for sheep during 2 consecutive summers sometime between 1922 and 1928 (Driscoll 1964).

Both the Canadian Bench and Western Peninsula are more typical of central Oregon rangelands in terms of their disturbance history and current use. Grazing is active on both sites (B. Cheney, Ochoco National Forest, pers. comm. 1995, S. Lusk, Ochoco National Forest, pers. comm. 1995, field reconnaissance 1997). For example, in 1994 there were 100 head of cattle grazing in the area containing the Canadian Bench study site and from the early to mid 1980s there also was horse grazing on the Canadian Bench. Horse Grazing on the Canadian Bench resumed again during the winter of 1994–1995. Records indicate that grazing on the Western Peninsula has been exclusively cattle since 1960 and an analysis of aerial photographs shows that an unimproved road was developed on the Western Peninsula study site sometime between 1961 and 1972. Although we know both sites have been grazed since 1960, it is not possible to reconstruct fully the domestic grazing history of either site beyond 1960 because of a lack of records. However, we do know that all but the most inaccessible central Oregon rangelands (e.g., the Island Research Natural Area) have been grazed intermittently since the late 1880s (Hopkins and Kovalchik 1983), so it is logical to conclude that both the Western Peninsula and Canadian Bench have been impacted by domestic grazing, at least intermittently, for over a century. In addition, we know that homesteading occurred in the area containing the Canadian Bench and Western Peninsula from the 1880s till the 1930s, and range conditions may have been altered by other anthropogenic activities such as prescribed fires, cutting and chaining of juniper, and seeding (e.g, some of the range in the area including the Canadian Bench was seeded with crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) in the 1930s and the 1960s).

The 3 study sites lie in a Fire Occurrence Zone of .03 to .07 fires/405 ha/yr, which places them in a low to medium range (K. Donham, Ochoco National Forest, pers. comm. 1995). However, large hot fires, such as the Little Cabin wildfire of August 1996 that burned 987 ha on land adjacent to the study sites before being contained, do occur within the region. Organized fire suppression is active on both the Western Peninsula and Canadian Bench, but not active on the Island Research Natural Area. National Fire Management Analysis fire records extend back to 1970, and these records show no fires on the 3 sites. However, interviews with personnel from the BLM, the Ochoco National Forest, and rangers at Cove Palisades State Park (which includes the Island Reseach Natural Area) revealed that 2 fires occurred on the Island Research Natural

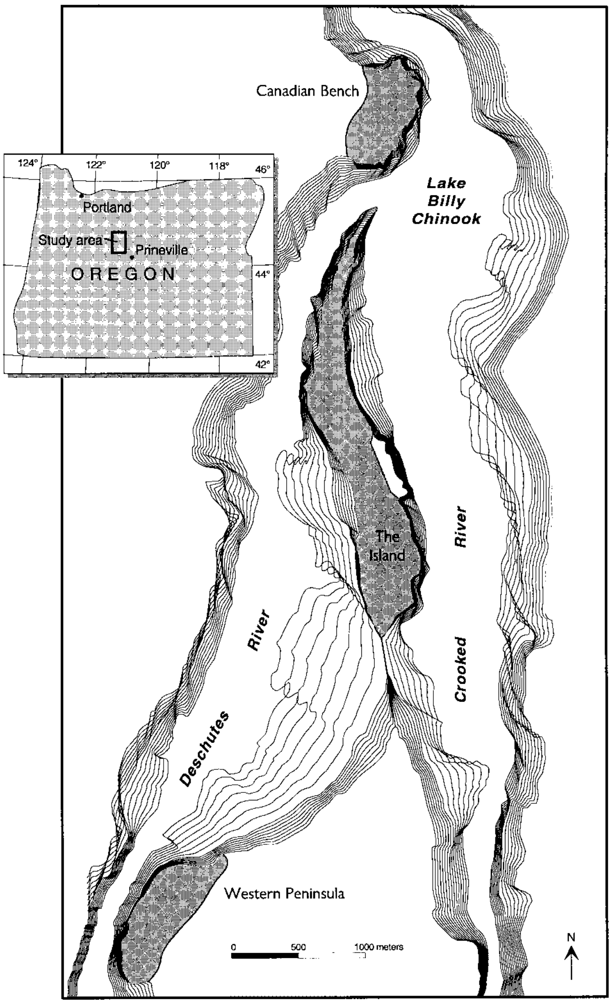

Fig. 1. Location of study sites and Prineville.

Area between 1970 and 1994, both on the same day in late August 1987. One fire burned an individual juniper before extinguishing, the second burned one-thirtieth of a hectare (Knapp and Soulé 1996).

Because all 3 sites are largely flat, at the same elevation (730 m), and separated by less than 3 km, their macroclimates should be identical. Records from Prineville, Ore. (Fig. 1) show the climate to be semiarid, with annual means of 25 cm for precipitation and 8.5°C for temperature. Prineville temperatures range from a mean of 18.1°C in July to –0.4°C in January, and precipitation ranges from a low of 0.99 cm in July to a maximum of 3.05 cm in November (Karl et al. 1990).

Soils characteristics on the 3 sites are similar, with loess as the parent material, thick loams (25 cm–40 cm) for the topsoil and subsoil, a topsoil to subsoil ratio of 0.5/1, and 1–2% organic matter (USDA-NRCS in press). The soil series for the Canadian Bench and Western Peninsula is Agency Madras, and for the Island Research Natural Area it is Agency Sandy. The 3 sites all support a *Juniperus occidentalis, Artemesia tridentata, Agropyron spicatum* plant community (Franklin and Dyrness 1988). On the Island Research Natural Area this is the dominant plant community, covering the 67 ha examined in this study. It is the sole community on the 29 ha examined on the Canadian Bench and the 34 ha examined on the Western Peninsula.

One change in the local environment occurred in 1963 with the damming of the Crooked and Deschutes Rivers to create Lake Billy Chinook. As detailed by Knapp and Soulé (1996), it is unlikely the creation of this lake altered the microclimate of the region in any manner significant to vegetation growth.

Methods

Vegetation

Using techniques detailed by Knapp et al. 1990, we monitored changes in both cover and density of trees through time using large scale (1:12,000 to 1:19,900) aerial photographs of the 3 study sites for the years 1951, 1956, 1961, 1972, 1982, and 1994. For each year and for each site the boundaries were delineated and 3 separate counts of western juniper density were made, with the average of the 3 counts presented in per hectare format. Scale limitations of the aerial photographs limit the density and cover measurement to mature western juniper. These observations are possible because of the uniformity of the vegetation associations and the lack of tree species diversity on the 3 sites.

Western juniper cover also was measured for each site and year using the dot-grid method (Poulton 1975). A dot grid (11 dots/cm^2) was overlaid on the photos. Each time a dot intersected a juniper the point was recorded. The total number of intersected dots (those overlaying or intersecting western juniper) divided by the total number of dots in the study area provides the cover estimate in percent. Three counts were made for each photograph, with cover being presented as the average of the 3.

Climate

To characterize climate, data from the Prineville 4NW station were used. Approximately 43 km to the southeast and 140 meters higher, Prineville 4NW is the closest and most comparable site in the Historical Climate Network database (Karl et al. 1990). Historical Climate Network data are desirable because of their high level of quality control and because they are corrected for biases (e.g., time of observation bias) that exist in most temperature and precipitation data sets for United States stations (Karl et al. 1990). Monthly temperature and precipitation data were compiled for the period July 1900 to June 1995. Missing data (<1.2%) were replicated as described by Knapp and Soulé (1996). We examined seasonal water year (July to June) and winter (November to February) trends for 1900–1994, for the period corresponding to our aerial photographs (1950–1994), and the prior period (1900–1949). We used November to February as winter because this includes 3 of the 4 wettest months (November, December, January) and accounts for 44% of annual precipitation, on average. We used linear regression to establish the direction of trend (e.g., Karl and Heim 1990, Plantico et al. 1990, Idso and Balling 1992, Soulé and Yin 1995), and tested for significance using rank correlation (Yin 1993). We tested for significant differences in seasonal water year and winter precipitation and temperature between the time period corresponding to aerial photographs (1950–1994) and the prior time period of available climate data (1900–1994) using the Wilcoxon Ran Sum W Test, a null hypothesis of no significant difference, and $\alpha = 0.05$.

Results

Vegetation

Density of mature western juniper increased at all sites from 1951 to 1994 (Figs. 2–5). The smallest absolute increase (3.13 trees/ha from 1951 to 1994, 210 trees total) occurred on the least disturbed site (the Island Research Natural Area). While the per hectare increase is nearly identical to that observed on the Western Peninsula (3.15 trees/ha, 107 trees total), the change in juniper density at the Canadian Bench (6.83 trees/ha, 198 trees total) is more than double that found at either the Island Research Natural Area or Western Peninsula. Absolute cover also increased from 1951 to 1994 at all sites, with the largest changes again found on the Canadian Bench (Fig. 6). Absolute cover changes at the Island Research Natural Area (3.3% increase from 1951 to 1994) were again more comparable to those observed on the Western Peninsula (4.8%) than the Canadian Bench (8.0%), but the relative (to 1951) cover changes were largest at the Western Peninsula (117% increase) and most similar between the Island Research Natural Area (60%) and the Canadian Bench (69%).

Climate

Long-term trends (1900–1994) of seasonal water year (SWY) precipitation are significantly upward, and both seasonal water year and winter precipitation are significantly greater in the 1950–1994 period compared to 1990–1949 (Table 1). However, within the time period corresponding to aerial photography analysis (1950–1994), precipitation is constant, and temperature is trending upward significantly (Table 1, Figs. 7 and 8). Winter precipitation is also greater from 1950–1994 than from 1900–1949 (Table 1), and winter temperature trends are nearly flat for all 95 years (Figs. 7 and 8). No significant differences were found for seasonal water year or winter temperatures between the 1950–1994 and 1900–1949 periods (Table 1).

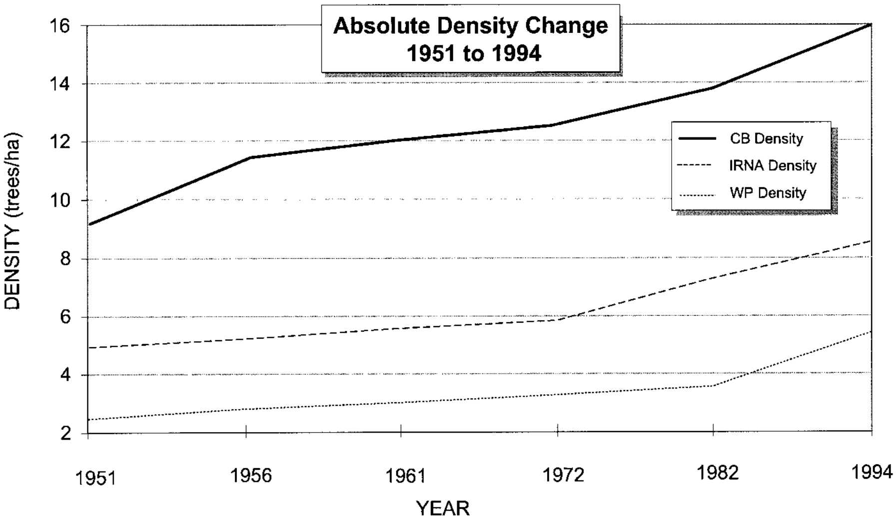

Fig. 2. Density changes of mature western juniper at the study sites from 1951 to 1994.

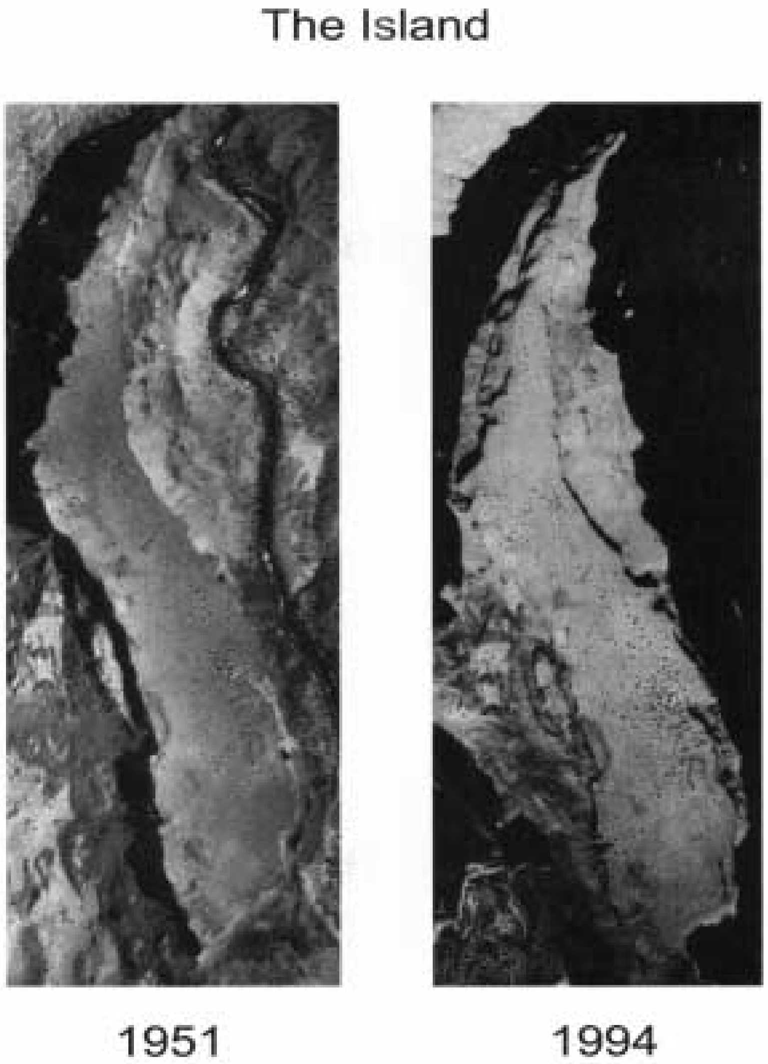

Fig. 3. Scanned images of black-and-white aerial photographs of the Island Research Natural Area for 1951 and 1994.

Discussion

Traditionally-cited causal mechanisms for western juniper expansion

Lack of fire is one of the 3 traditional mechanisms cited for western juniper expansion

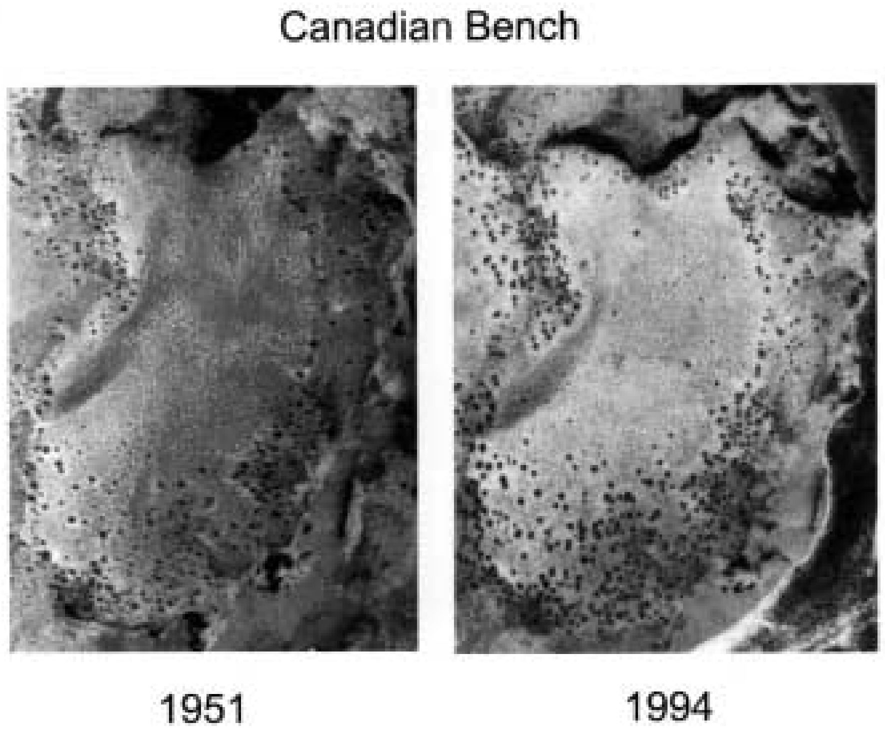

Fig. 4. Scanned images of black-and-white aerial photographs of the Canadian Bench for 1951 and 1994.

that may have impacted our study sites. Western juniper is a "fire avoider" and tree mortality is high during the seedling and sapling stage (Agee 1993:385). Field reconnaissance of the area burned in the Little Cabin fire of 1996 showed almost complete mortality of western juniper of all ages. Clearly there have been no fires of this magnitude on the 3 sites during the time period of available aerial photographs (1951–1994), and a lack of large numbers of burned stumps on the sites suggests the fire-free interval (for major fires) extends well before 1950. While the lack of grazing on the Island Research Natural Area should lead to a differential susceptibility to fire, the fire history of the past half century or more appears to have been equally beneficial to wesern juniper expan-

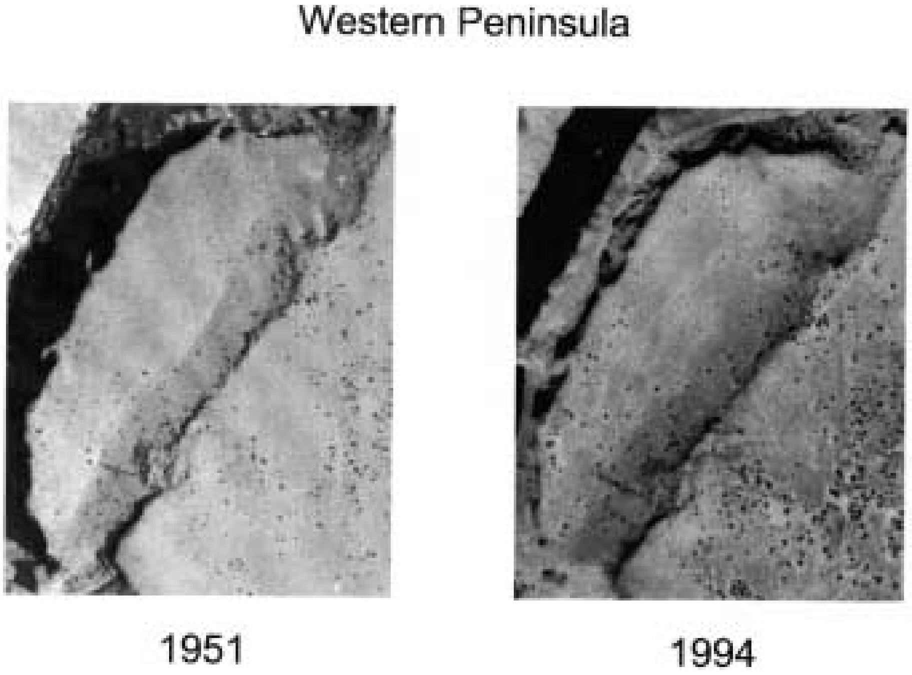

Fig. 5. Scanned images of black-and-white aerial photographs of the Western Peninsula for 1951 and 1994.

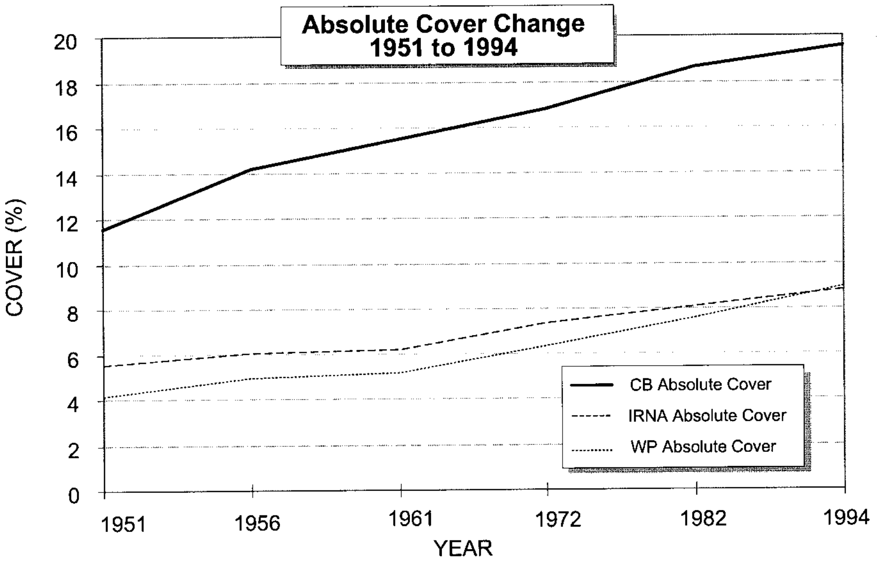

Fig. 6. Cover changes of mature western juniper at the study sites from 1951 to 1994.

sion on all 3 sites. Additional evidence suggests that altered fire regimes (fuel reduction from domestic livestock grazing and/or fire suppression) are not required for juniper expansion, since expansion and contraction of western juniper range and density occurred for several millennia prior to widespread anthropogenic activities (Miller and Wigand 1994).

Livestock grazing on the Canadian Bench and Western Peninsula may have influenced increases in western juniper density and cover by reducing perennial grass cover, thereby altering fire regimes (Miller et al. 1994) and perhaps improving juniper seedling establishment via a decrease in interspecific competition (in Miller et al. 1994). Archer (1994:13) has chiefly implicated livestock grazing as the "primary force" for causing woody plant invasions into southwestern grasslands and savannas and suggested that the greatest influence of livestock grazing on woodland encroachment may be on the establishment of woody plant seedlings. While there is little evidence that reduced perennial grass cover competition has facilitated western juniper establishment (Burkhardt and Tisdale 1976, Young and Evans 1981, Miller et al. 1994), it has been suggested that increased *Artemesia tridentata* cover has favored juniper seedlings by creating preferential microclimatic habitats (Eddleman 1987). Expansion of shrubs does occur in the absence of grazing in central Oregon, as Knapp and Soulé (1996) reported a near doubling of *Artemesia tridentata* cover from 1960 to 1994 on the Island Research Natural Area. While livestock grazing cannot adequately explain changes in western juniper density and cover on the Island Research Natural Area, these results are consistent with other findings (e.g., Anderson and Holte 1981, Goldberg and Turner 1986, Knapp and Soulé 1998) in that ongoing grazing is not a required mechanism to promote increasing woodiness on arid western rangelands.

The analyses of macroclimatic conditions provide mixed results. Miller and Rose (1995) speculate that the wetter, milder winters that occurred from 1850 to 1916 helped sustain growth and were a contributing factor to historic western juniper expansion in southeastern Oregon. Our analyses of precipitation at Prineville show that winter precipitation was significantly higher in the 1950–1994 period compared to the 1900–1949 period, a situation potentially beneficial to increased growth in the later half of the century. However, the

Table 1. Characteristics, trends, and time period comparisons for seasonal water year (SWY) and winter (Win.) temperature and precipitation. Data are from the Prineville 4NW station.

Time Period	Wilcoxon Test p-value	Variable	N	Mean	Regression SD	Spearman Slope	Spearman rs	p-value rs
precipitation:			(mm)					
1900–1994		SWY ppt	95	25.0	6.5	0.0515	0.22	0.035
1900–1949	0.018	SWY ppt	50	23.4	5.1	0.0243	0.08	0.583
1950–1994		SWY ppt	45	26.7	7.5	–0.0415	–0.06	0.689
1900–1994		Win. ppt	95	10.9	4.1	0.0271	0.20	0.051
1900–1949	0.005	Win. ppt	50	9.8	3.5	–0.0109	–0.07	0.643
1950–1994		Win. ppt	45	12.1	4.5	–0.0652	–0.18	0.233
temperature:			(°C)					
1900–1994		SWY temp	95	8.5	0.7	0.0009	0.05	0.623
1900–1949	0.260	SWY temp	50	8.4	0.8	–0.0213	–0.39	0.006
1950–1994		SWY temp	45	8.5	0.6	0.0164	0.34	0.021
1900–1994		Win. temp	95	1.5	1.4	–0.0002	0.07	0.514
1900–1949	0.060	Win. temp	50	1.3	1.3	–0.0273	–0.28	0.052
1950–1994		Win. temp.	45	1.7	1.4	–0.0197	–0.13	0.405

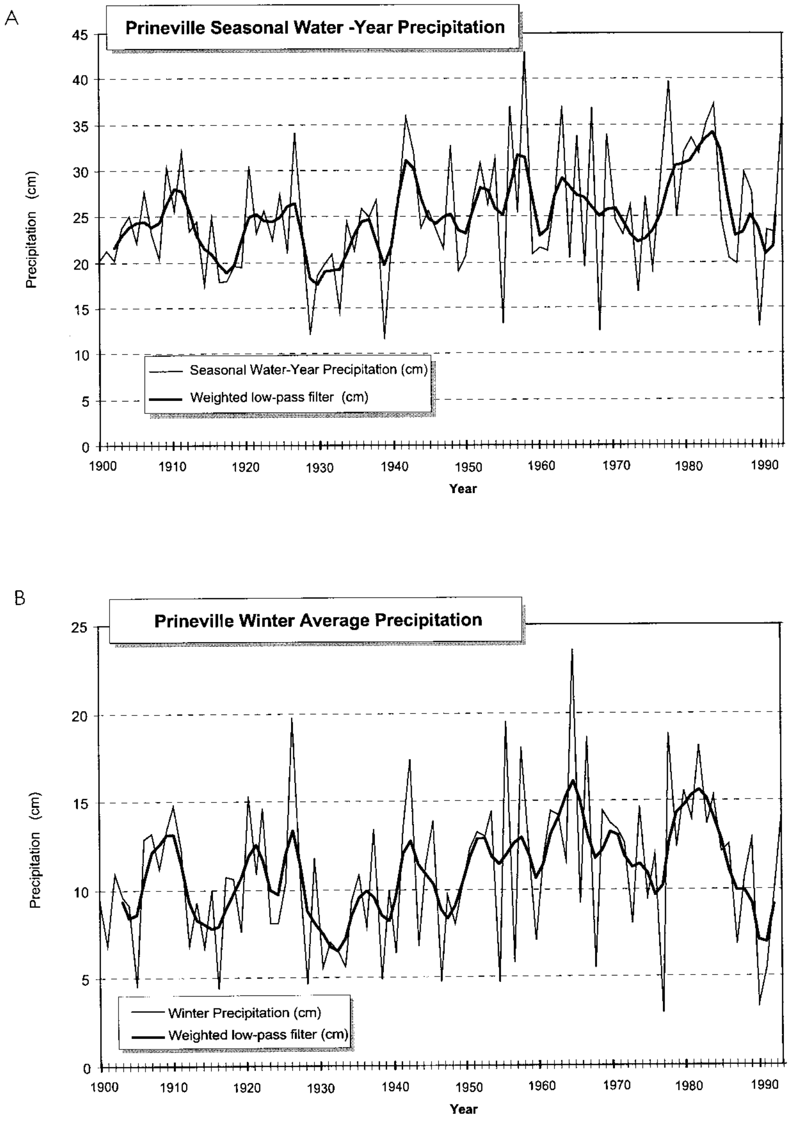

Fig. 7. Seasonal water-year precipitation and winter precipitation for Prineville, Ore.

later period displays considerable inter-yearly and inter-decadal variability, with 2 periods (mid 1960s–late 1970s; 1980s) of sharply falling winter precipitation, and the 2 driest winters since 1900 (1976, 1989)

Despite higher mean precipitation values in the 1950–1994 period, the data do not appear to implicate climatic conditions as a major cause of juniper expansion from 1950–1994 on the study sites. Juniper density and cover have consistently increased during this time period while precipitation has been more erratic (higher standard deviation), compared to the first half of the century. Because of their slow growth rates (Bedell et al. 1993), it is likely that many of the juniper observed in the 1951–1994 aerial photographs established during the early portion of the century, when conditions were (on average) drier at nearby Prineville (Table 1), or during the more favorable periods for establishment of the late 1800s shown on various western juniper chronologies for the surrounding region (Holmes et al. 1986) . We also note that patterns of establishment and expansion throughout central (e.g., Eddleman 1987) and southeastern Oregon (Miller and Rose 1995) have trended upward since the late 1800s under varying climatic conditions, and that density and cover values have accelerated from the 1950s.

Alternative causal mechanisms for western juniper expansion

Our results, showing increases in density and cover, are in basic agreement to what has been shown for the entire western juniper woodland range (e.g., Burkhardt and Tisdale 1976, Young and Evans 1981, Eddleman 1987, Miller and Wigand 1994, Miller and Rose 1995) . These studies have suggested that livestock grazing and/or altered fire regimes are likely the major causes for these shifts. Domestic livestock grazing and active fire suppression, along with climatic fluctuations, however, appear inadequate for explaining fully the changes observed on the Island Research Natural Area.

What then can explain the western juniper increases on the Island Research Natural Area? Despite a lack of organized fire suppression, there have not been any fires of significant areal influence since 1951 (and probably much longer) on the Island Research Natural Area. Thus, the current expansion on the Island Research Natural Area may simply be an artifact of the same fire-free period as that experienced on the more disturbed sites. We suggest that on near-relict sites such as the Island Research Natural Area, the rare combination of sufficient fine fuel accumulation and weather conditions necessary to promote and carry hot fires are infrequent enough to be only marginally consequential to inhibit juniper expansion.

Increases on all sites also may be a result of biological inertia (Miller and Rose 1995), which is partially manifested through increased seed rain. Western juniper typically reach full reproductive maturity at approximately 75 years of age (Bedell et al. 1993) . Thus, some of the increases in density and cover observed on the aerial photographs may be attributed to higher female cone production as many of the trees established decades ago during more favorable climatic conditions (e.g., late 1800s) reach reproductive maturity.

Our field reconnaissance of the study sites indicates that the majority of western juniper have prodigious berry production, and the ratio of juvenile (all awl-like foliage) to mature western juniper (all scale-like foliage) is large. While quantification of these observations was beyond the scope of this study, we can circumstantially infer that an increasing seed rain is a potential fac-

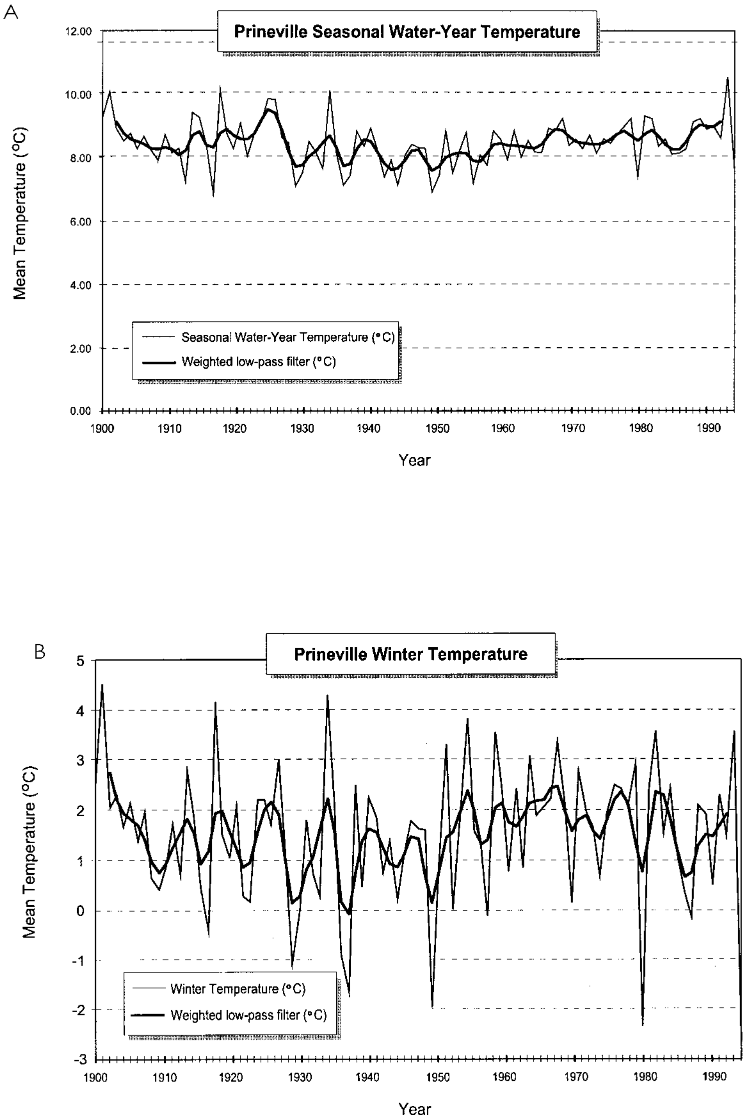

Fig. 8. Seasonal water-year temperature and winter temperature for Prineville, Ore.

tor in the observed density increases on the study sites from 1951–1994, and that, in the absence of a catastrophic fire, density will continue to increase as the juvenile population matures.

An additional possibility for western juniper expansion is increased seed dispersal (Archer 1994). That is, even in areas where domestic grazing has not occurred, and fire regimes have not been altered, an increase in cone production from nearby sites could result in expansion. In southwestern Idaho, Burkhardt and Tisdale (1976) found that western juniper seed dispersal primarily occurred downslope because of gravity and was spatially limited with an average maximum dispersal (during the summer) of 1.42 m. Dispersion by birds and mammals also was considered, but Burkhardt and Tisdale (1976) noted that the scarcity of disjunct western juniper stands in their study area suggested only a minor role for animal dispersion. Because the Island Research Natural Area is geographically isolated from the denser western juniper woodlands that surround it, seed dispersal would appear to play only a minimal role in the observed expansion.

It has been suggested that increasing levels of atmospheric CO_2 also may have influenced western juniper expansion (e.g., Miller and Wigand 1994, Knapp and Soulé 1998). In general, most species (particularly woody plants) may benefit from elevated CO_2 through increased photosynthesis, and/or reduced transpiration, thus increased water-use efficiency (Idso 1989, Idso and Kimball 1993). Juvenile western juniper appear physiologically well-suited to exploit atmospheric CO_2 (Miller et al. 1992, 1995). Miller et al. (1995:478) suggest that this physiologic advantage should both "enhance establishment and early growth," and increase the ability of juvenile western juniper to compete with other species. While tree growth exceeding that expected by climate in the later half of the twentieth century (when atmospheric CO_2 rates have increased most rapidly) has not (to our knowledge) yet been established for western juniper through dendroecological analyses, growth exceeding that expected by climate has been documented for some western coniferous species (e.g., LaMarche et al. 1984, Graybill and Idso 1993), opening the door for speculation that CO_2 enrichment is a possible contributing factor to western juniper expansion.

Conclusions

Western juniper expansion has profound management implications that must be addressed by the BLM and other governmental agencies (Evans 1988, Bedell et al. 1993, Haugen 1993, Liverman 1993) . This study shows that western juniper expansion can occur on lands with varied land use histories, on the arid end of its range, and on land that is not downslope from its founding population. Our results suggest that the mechanisms traditionally proffered to explain the post 1800s expansion of western juniper (i.e., domestic grazing, altered fire regimes, favorable climatic conditions) are not necessarily required to sustain expansion. Because the processes involved in western juniper afforestation are likely synergistic and site specific (Liverman 1993), the search for causal mechanisms should continue to include all potential elements that affect the dynamics of western juniper woodlands.

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52:534–538 September 1999

Imbibition temperature affects on seedling vigor: In crops and shrubs

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Abstract

Imbibition at cold temperatures reduces seedling vigor of some species, but is beneficial to others. We used 3 rangeland shrubs and 8 agronomic crop species to test for a general relationship between imbibition temperature (5 to 30°C) and seedling vigor measured as post-germination growth; and to test for an effect of imbibition temperature on seed water uptake and dry weight loss during imbibition. Imbibition temperatures between 5 and 15°C were correlated with greater seedling length of the shrubs while most crops were favored by imbibition temperatures between 20 and 30°C. Winter wheat (*Triticum aestivum* L.) response to imbibition temperature was similar to that of the shrubs. Generally, shrubs had lower post-germination growth than crops, and during imbibition most crop seeds lost less weight than shrub seeds. Winter wheat had high weight loss as well as high seedling vigor. Seed water content generally increased with increasing imbibition temperature; however, winter wheat, kochia (*Kochia prostrata* (L.) Schrad.), and big sagebrush (*Artemisia tridentata* Nutt.) had significantly less water when imbibed at 30°C than when imbibed at lower temperatures. The differences due to temperature suggest the relationship between imbibition temperature and seedling vigor is a general phenomenon related to the physiology of water uptake and to seed respiration (as indicated by weight loss). Therefore, we recommend that optimum imbibition temperatures be defined by species and incorporated into seed-testing guidelines. This appears particularly important for species that do not have a long history of cultivation and whose response to temperature may differ significantly from that of crops.

Key Words: imbibition damage, germination, post-germination growth, imbibition weight loss, seed testing

Resumen

La imbibición a bajas temperaturas reduce el vigor de las plántulas de algunas especies y es benéfica para otras. Utilizamos 3 arbustos de pastizal y 8 especies cultivadas para probar una relación general entre la temperatura de imbibición (5 a 30°C) y el vigor de la plántula (medido como crecimiento post-germinación) y para probar el efecto de la temperatura de imbibición en la absorción de agua de la semilla y perdida de peso seco durante la imbibición. Las temperaturas de imbibición entre 5 y 15°C se correlacionaron con una mayor longitud de la plántula de los arbustos mientras que la mayoría de los cultivos respondieron mejor a las temperaturas de imbibición entre 20 y 30°C. La respuesta del trigo invernal (*Triticum aestivum* L.) a la temperatura de imbibición fue similar a la de los arbustos. Generalmente los arbustos tienen menor crecimiento post-germinación que las especies cultivadas y durante la imbibición la mayoría de las semillas de los cultivos pierden menos peso que las semillas de arbustos. El trigo invernal tuvo una alta perdida de peso y un vigor de plántula alto. El contenido de agua de la semilla generalmente se incrementa al incrementar la temperatura de imbibición, sin embargo, el trigo invernal, kochia (*Kochia postrata* (L.) Schrad), y big sagebrush (*Artemisa tridentata* Nutt.) tuvieron un contenido de agua significativamente menor cuando se imbibieron a 30°C que cuando se imbibieron a temperaturas más bajas. Las diferencias debidas a la temperatura sugieren que la relación entre la temperatura de imbibición y el vigor de plántula es un fenómeno general relacionado a la fisiología de absorción de agua y la respiración de la semilla (Tal como lo indica la perdida de peso). Por lo tanto, recomendamos que la temperatura óptima de imbibición se sea definida por especie e incorporada en las guías de pruebas de semilla. Esto parece ser particularmente importante para especies que no tienen un largo historial de cultivo y cuya respuesta a la temperatura puede deferir significativamente de otros cultivos.

Seed (or seedling) vigor is a condition of active good health that permits germination and early growth to proceed rapidly and completely (Justice and Bass 1978). Vigor, measured as post-germination growth, is generally reduced by imbibition at cold temperatures for common agronomic species (Vertucci 1989, Bradford 1995). Low imbibition temperature reduces seedling vigor in lima bean (*Phaseolus lunatus* L.) (Woodstock and Pollock 1965, Pollock 1969), bush bean (*Phaseolus vulgaris* L.) (Pollock et al. 1969, Roos et al. 1976), cucumber (*Cucumis sativus* L.) (Segeta and Tronickova 1966, Jennings and Saltveit 1994), pea (*Pisum sativum* L.) (Highkin and Lang 1966), and many other important crops with tropical or subtropical origins (Lyons 1973). Imbibition at 5°C for 30

Authors thank Dr. N.L. Shaw for supplying hopsage seeds, L.W. Griffith for technical assistance, and Drs. M.A. Cohn, M.B. McDonald and E.E. Roos for reviewing this manuscript. Mention of trade or company names is for information only and does not imply an endorsement.

Manuscript accepted 19 Oct. 1998.

minutes reduced oxygen uptake of lima bean seedling axes by 20 to 40% relative to imbibition at 25°C (Woodstock and Pollock 1965), with injury at 5°C being related to the moisture content of the seed (Pollock 1969). By contrast, some seeds such as spiny hopsage (*Grayia spinosa* (Hook.) Moq.) (Smith 1974, Shaw et al. 1994), kochia (*Kochia prostrata* (L.) Schrad.) (Haferkamp et al. 1990), winterfat (*Eurotia lantata* (Pursh) Moq.) (Booth 1992), and cold resistant maize (*Zea mays* L.) cultivars (van de Venter and Grobbelaar 1985), can have greater seedling vigor after cold (0 to 10°C), compared to warm (>15°C), imbibition temperatures. To determine if there is a general correlation between imbibition temperature and seedling vigor, we tested 3 rangeland shrubs and 8 agronomic crop species and measured the effects of imbibition temperature on post-germination growth and how growth is related to seed water uptake and weight loss during imbibition.

Materials and Methods

Seed Sources

Seeds were obtained from commercial sources except for spiny hopsage and kochia, which were collected from Oregon and Utah, respectively (Table 1). Seed weights ranged from 0.028 g per 100 seeds for spiny hopsage to 32.55 g per 100 seeds for bush bean. After purchasing or harvesting, seeds were stored at room temperature. Seed weight on a dry weight basis was determined at the beginning of each study.

Water Uptake and Weight Loss of Seed /Seedlings During Imbibition at VariousTemperatures

Seeds of each species were divided into 5 groups or replications. The number of seeds per group ranged from 10 (pea, bean, etc.) to 140 (hopsage), depending on the number of seeds needed to exceed a minimum group weight of 0.05 g (0.04 g for hopsage due to our limited supply). The seed groups of each species were weighed to 0.01 mg, then dried at 35°C for 7 days. This procedure was designed to obtain a stable "dry" weight without damaging the embryos (Booth 1992). Seeds were humidified by placing them above distilled water in a closed container at 2°C until seed moisture content exceeded 10% as determined by daily weighing. This was done to standardize seed moisture and reduce the chance of imbibitional injury (Pollock 1969, Vertucci and Leopold 1984). Humidified seeds were mounted on slant boards (Jones and Cobb 1963), placed in closed 25 x 40 x 21 cm plastic boxes, and then imbibed for 4 days in incubators at 5, 10, 15, 20, 25, or 30°C. After imbibition, seeds/seedlings were dried as described above and the percent weight loss during the 4-day imbibition was calculated on a dry weight basis. The experimental design was a randomized complete block design (RCBD). Data (n=5) were analyzed separately for each species using analysis of variance (ANOVA) and means were compared with the Least Significant Difference (LSD) where there was a significant F statistic for treatment effects (Snedecor and Cochran 1980). Temperature is a continuous variable; however, some seed responses suggest biological thresholds that produce discrete responses which are better analyzed by ANOVA and LSD.

Seed Germination and Seedling Vigor in Relation to Imbibition Temperature

Twenty humidified seeds were mounted on slant boards, placed in closed plastic boxes, and then imbibed for 4 days in incubators at 5, 10, 15, 20, 25, or 30°C. They were then incubated at constant or alternating temperatures in darkness for 7 days for crops, or 14 days for shrubs, as recommended by the Association of Official Seed Analysts (AOSA 1988) or Schopmeyer (1974). The incubation conditions were 20/30°C under 16/8 hours light/darkness for cucumber, sunflower (*Helianthus annuus* L.), tomato (*Lycopersicon pimpinellifolium*) Mill.), bush bean and hopsage;

Table 1. Description of seed sources and other characteristics for the 3 shrubs and 8 crop species examined in this study.

Species and cultivar	Age of seed (years)	Source	Seed weight (mean±SE/100 seeds)
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Spiny hopsage (*Grayia spinosa* (Hook.) Moq.)	4	Malheur, Ore.	0.028±0.002
Kochia (*Kochia prostrata* (L.) Schrad.	3	Sanpete, Ut.	0.106±0.002
Big sagebrush (*Artemisia tridentata* Nutt.)	1	Wind River Seed Co., Manderson, Wyo.	0.046±0.001
Cucumber, Straight Eight (*Cucumis sativus* L.)	1	Gurney's Seed Co., Yankton, S. Dak.	2.004±0.036
Sunflower, Black Stripe (*Helianthus annuus* L.)	1	Gurney's Seed Co., Yankton, S.Dak.	8.418±0.107
Tomato, Delicious (*Lycopersicon pimpinellifolium* Mill.)	1	Gurney's Seed Co., Yankton, S.Dak.	0.247±0.001
Bush Bean, Top Crop (*Phaseolus vulgaris* L.)	1	Gurney's Seed Co., Yankton, S.Dak.	
Pea, Alaska (*Pisum sativum* L.)	3	Gurney's Seed Co., Yankton, S.Dak.	9.310±0.321
Radish, Mr. Big (*Raphanus sativus* L.)	4	Gurney's Seed Co., Yankton, S.Dak	1.030±0.017
Spinach, Bloomsdale Long Standing (*Spinacia oleracea* L.)	1	Gurney's Seed Co., Yankton, S.Dak.	1.077±0.018
Winter Wheat, Buckskin (*Triticum aestivum* L.)	2	Wyo. Certified Seed, Univ. Wyo., Laramie	3.477±0.006

Table 2. Seed/Seedling water content on dry weight basis of 3 shrub and 8 crop species after 4 days of imbibition at various temperatures.

Species	Imbibition temperature (°C)					
	5	10	15	20	25	30
	%					
Grayia spinosa	132 a[1]	165 a	181 a	180 a	210 a	201 a
Kochia prostrata	190 c	186 c	400 a	335 ab	275 b	182 c
Artemisia tridentata	156 d	213 cd	345 ab	373 a	282 abc	240 bcd
Cucumis sativus	61 d	65 d	64 d	182 c	494 b	726 a
Helianthus annuus	59 e	80 e	125 d	202 c	314	423 a
Lycopersicon pimpinellifolium	94 d	91 d	96 d	128 c	235 b	298 a
Phaseolus vulgaris	88 e	98 de	105 d	133 c	194 b	225 a
Pisum sativum	102 d	110 d	137 c	197 b	219 a	215 a
Raphanus sativus	85 d	160 d	376 c	1105 b	1512 a	1478 a
Spinacia oleracea	78 c	83 bc	87 bc	99 b	121 a	93 bc
Triticum aestivum	76 d	216 c	355 a	192 c	273 b	214 c

[1] Means with the same letters within a species across temperatures are not significantly different at P≤0.05 according to LSD.

20°C in darkness for pea, radish (*Raphanus sativus* L.) and kochia; and 15°C in darkness for spinach (*Spinacia oleracea* L.) and big sagebrush (*Artemisia tridentata* Nutt). Germinated seeds were counted, and seedling axial lengths measured at 3, 5, and 7-day intervals for crops; and at 5, 7, 10, 12, and 14 -day intervals for shrubs. We used the maximum seedling axial length to assess seedling vigor (Booth and Griffith 1994). The randomized complete block design (RCBD) was used with 5 replications arranged over time so that no 2 replications of a species were tested simultaneously. Data for each species were analyzed for germination and axial length.

Results and Discussion

Water Uptake of Seed/Seedling During Imbibition

The water content of seeds and seedlings after 4 days of incubation ranged from 61 to 1,512%, depending on species and imbibition temperature (Table 2). Many seeds of crops germinated during the 4-day period. This is important since these seeds may have had greater respiration rates than ungerminated seeds. The variation in water content among temperatures was inversely related to seed size. For example, the variation was smaller in species with larger seeds such as sunflower, bean, and pea, than species with smaller seeds. The water uptake for cucumber, sunflower, tomato, and bean seeds increased with increasing imbibition temperatures, while spinach, winter wheat (*Triticum aestivum* L.), kochia, and big sagebrush seeds imbibed significantly less water at 30°C than at lower temperatures.

Seeds generally absorb water more slowly at lower temperatures (Shull 1920, Allerup 1958, Bai et al. 1999), which is attributed to increased viscosity of water with decreasing temperature, and to the effect of temperature on seed membranes (Murphy and Noland 1982, Vertucci and Leopold 1983, Vertucci 1989). Vertucci (1989) discussed the effect of seed microstructure on water uptake, commenting that temperature was likely to alter that structure. These reports and others (Bewley and Black 1978), discuss imbibition within the context of a linear relationship between increasing temperature and increasing rate of seed moisture uptake. The exceptions to that relationship found in this study, and similar findings by Bai et al. (1997), hint of biochemical differences among seeds with different temperature responses. These differences need to be better understood.

Dry Weight Loss of Seed/Seedling After Imbibition

Weight losses during imbibition ranged from 0.7 to 50.1%, and generally increased with increasing imbibition temperatures (Table 3). Sunflower showed greater weight loss at 20 than at 30°C, and bush bean showed no differences among temperatures. We specu-

Table 3. Percent of seed/seedling dry weight loss of 3 shrub and 8 crop species after 4 days of imbibition at various temperatures.

Species	Imbibition temperature (°C)					
	5	10	15	20	25	30
	%					
Grayia spinosa	24.3 cd[1]	20.8 d	18.6 d	30.4 bc	38.5 ab	43.7 a
Kochia prostrata	8.4 d	13.1 cd	19.2 c	28.9 b	44.6 a	50.1 a
Artemisia tridentata	10.7	—	13.4	—	21.8	—
Cucumis sativus	1.4 b	1.6 b	1.9 b	2.4 a	2.3 a	2.8 a
Helianthus annuus	0.7 c	1.3 b	1.7 ab	2.2 a	1.7 ab	1.6 b
Lycopersicon pimpinellifolium	2.5 b	2.1 b	2.6 b	1.7 b	4.7 a	5.6 a
Phaseolus vulgaris	1.7 a	2.5 a	2.5 a	4.0 a	3.6 a	3. 1 a
Pisum sativum	1.3 de	2.1 de	3.6 d	5.7 c	8.4 b	10.2 a
Raphanus sativus	0.9 d	6.7 bc	1.6 d	3.7 cd	7.1 b	11.3 a
Spinacia oleracea	3.3 c	3.9 bc	4.3 bc	4.6 b	5.6 a	6.3 a
Triticum aestivum	2.6 d	9.3 c	23.1 b	11.4 c	20.2 b	34.0 a

[1] Means with the same letters within a species across temperatures are not significantly different at P≤0.05 according to LSD.

Table 4. Germination percentage of 3 shrub and 8 crop species incubated at recommended temperatures.

Species	Imbibition temperature (°C) 5	10	15	20	25	30
	%					
Grayia spinosa	16[1]	29 a	21 a	23 a	25 a	25 a
Kochia prostrata	67 a	71 a	73 a	77 a	78 a	44 b
Artemisia tridentata	82 a	73 ab	80 ab	82 a	70 bc	59 c
Cucumis sativus	92 a	95 a	95 a	98 a	97 a	95 a
Helianthus annuus	94 a	95 a	94 a	94 a	89 a	84 a
Lycopersicon pimpinellifolium	96 a	98 a	94 a	94 a	92 a	95 a
Phaseolus vulgaris	99 a	99 a	99 a	99 a	97 a	99 a
Pisum sativum	96 a	98 a	98 a	97 a	99 a	97 a
Raphanus sativus	100 a	95 a	95 a	99 a	98 a	98 a
Spinacia oleracea	76 ab	74 ab	82 a	64 b	65 b	46 c
Triticum aestivum	94 ab	97 a	98 a	95 ab	90 b	84 c

[1] Means with the same letters within a species across temperatures are not significantly different at P≤0.05 according to LSD.

late that sunflower seeds may have respiration controls that act to conserve food during germination at temperatures higher than optimum for growth, i.e., respiration was inhibited by high temperature. Weight losses were generally smaller for crops than shrubs, except in winter wheat, and larger-seeded species tended to lose relatively less weight than smaller seeded species.

Booth and Haferkamp (1995) reviewed 33 reports published between 1954 and 1988 that correlated seed size (best measured as seed weight) with dicot or monocot seedling vigor. These reports indicate that greater seed size within a species was correlated with greater seedling vigor. Booth (1992) found that post-imbibition dry seed weight was a better predictor of post-germination growth of winterfat than the pre-imbibition seed weight. Because the post-imbibition seed weight is an index of the amount of food remaining for seedling growth after the stressful imbibition period, it will be more closely related to post-germination growth than the pre-imbibition seed weight.

Seed Germination as Affected by Imbibition Temperature

Except for spinach, winter wheat, kochia, and big sagebrush, germination was generally high (>90%) and was not affected by imbibition temperature (Table 4). Hopsage germination was low and independent of imbibition temperature, possibly due to its low seed viability after a prolonged storage period. Higher temperatures reduced germination for spinach, winter wheat, kochia, and big sagebrush. This may reflect their temperate origins.

Seedling Vigor as Affected by Imbibition Temperature

Maximum seedling axial length occurred at the end of each experiment (7 or 14 days) for all temperatures and species except for big sagebrush and hopsage seeds imbibed at 30°C (Table 5). Here, maximum length occurred after 10 days of incubation. Post-germination growth increased with increasing imbibition temperature for cucumber and sunflower. It was optimum at 20 and 25°C for tomato and bush bean, at 25°C for pea, and at 15 to 25°C for radish. Low temperatures correlated with greater seedling axial length for winter wheat, hopsage, kochia, and big sagebrush. The benefits of low-temperature imbibition have been previously reported for hopsage (Smith 1974, Shaw et al. 1994) and kochia (Haferkamp et al. 1990).

Seeds with lower weight loss during imbibition had greater post-germination growth, and all crop species, except for winter wheat, fell into this category. Winter wheat had high weight loss as well as high seedling vigor. High weight loss in shrubs was associated with low

Table 5. Maximum average seedling lengths for 3 shrub and 8 crop species after incubation at recommended temperatures.

Species	Imbibition temperature (°C) 5	10	15	20	25	30
	%					
Grayia spinosa	8 b[1,2]	13 a[3]	15 a	7 b	8 b	5 b
Kochia prostrata	30 a	33 a	31 a	28 a	20 b	17 b
Artemisia tridentata	30 ab	31 a	27 ab	26 b	21 ce	20 d
Cucumis sativus	178 d	195 c	205 c	263 b	271 b	291 a
Helianthus annuus	227 c	281 b	290 b	399 a	361 a	341 a
Lycopersicon pimpinellifolium	127 c	120 c	146 b	175 a	182 a	150 b
Phaseolus vulgaris	285 c	280 c	346 b	466 a	447 a	366 b
Pisum sativum	239 e	265 d	291 c	288 b	316 a	293 b
Raphanus sativus	260 d	287 bc	301 ab	318 a	304 ab	273 c
Spinacia oleracea	112 ab	119 a	115 ab	97 b	105 ab	60 c
Triticum aestivum	336 a	292 b	263 bc	253 cd	227 d	222 d

[1] Maximum seedling length was reached after 7 days of incubation for crops and after 14 days of incubation for shrubs, except for *Grayia spinosa* and *Artemisia tridenta* which when imbibed at 30°C, reached maximum seedling length after 10 days of incubation.

[2] Means with the same letters within a species across temperatures are not significantly different at P≤0.05 according to LSD.

[3] Underline indicates values that are not different from maximum.

seedling vigor. These results are evidence that imbibition temperature influences (1) moisture uptake, (2) seed -weight loss during imbibition, (3) germination, and (4) seedling vigor.

Recent work in our laboratory has found that the age of winterfat seeds influences the vigor response to imbibition temperature (Booth et al. 1999). This raises the question of the effect of age on studies reported here. Since there are differences among species from equal-age seed, such as among cucumber, tomato, and spinach (Table 5), we suspect that species, age, and environment interact to define a vigor response to imbibition temperature.

We tested one seed lot for each of 11 species to assess general, rather than specific, responses. Our results suggest species differences, but do not define specific imbibition temperature responses. Our results do establish that there is a continuum in vigor responses to imbibition temperatures for a wide variety of seeds (Tables 2 and 5). Previous work has focused on chilling injury in plants of tropical or subtropical origins. We have shown an effect of imbibition temperature for those species, and for plants of temperate origin. The significance of these ecophysiological interactions on the dynamics of temperate plant populations in agronomic and wildland settings needs to be understood.

We conclude that seed -testing personnel seeking to measure full expression of seed growth potential must give attention to imbibition temperature as a distinct part of the germination protocol. We recommend that guidelines be developed for imbibing seeds and that these be incorporated into seed testing procedures recommended by the Association of Official Seed Analysts (AOSA), International Seed Testing Association (ISTA), similar organizations, and in published guidelines such as Agricultural Handbook 450 (Schopmeyer 1974). Perspectives in seed science and technology have been strongly influenced by crop species with long agronomic histories. This study has revealed differences in seed response to temperature for a wide variety of seeds. That information should broaden our perspective of seed testing, particularly as more and more rangeland plants come into the seed trade.

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J. Range Manage.
52:539-542 September 1999

Total nonstructural carbohydrate trends in Chinese tallow roots

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Abstract

Chinese tallow (*Sapium sebiferum* L. Roxb.) was introduced to the United States from China in the mid to late 1800s and has since naturalized throughout much of the southern U. S. Tallow continues to invade a wide variety of habitats, but control efforts have been inconsistent. We related root total nonstructural carbohydrate (TNC) levels and phenological development in Chinese tallow over an annual cycle to determine optimal timing for control treatments. Six phenological stages were recorded; (1) dormancy, (2) bud break, (3) leaf development, (4) seed formation, (5) seed maturation, and (6) leaf fall. Tallow root TNC concentrations varied by phenological stage ($P<0.001$), where concentrations were highest ($P <0.05$) during leaf fall (60.72%) and lowest during leaf development (41.11%) and seed formation (36.71%). Chinese tallow root TNC concentrations increased during the period of seed maturation until leaf fall. If foliar applied herbicides are delivered during this period of downward translocation, effective tallow control may be observed.

Key Words: exotic plant control; restoration; *Sapium sebiferum*; total nonstructural carbohydrate trends

Resumen

"Chinese tallow" (*Sapium sebiferum* L. Roxb.) fue introducido a Estados Unidos en la segunda mitad del siglo pasado y desde entonces se ha naturalizado en gran parte del sudeste de Estados Unidos. "Tallow" aun continua invadiendo una amplia variedad de hábitats, y los esfuerzos de control han sido inconsistentes. Relacionamos los niveles de carbohidratos noestructurales totales de la raíz (CNT) y el desarrollo fenológico del "Chinese tallow" a través del año para determinar la época óptima de aplicación de tratamientos de control. Se registraron 6 etapas fenológicas: (1) dormancia, (2) brotación de yemas, (3) desarrollo de hojas, (4) formación de semilla, (5) maduración de semilla y (6) caída de hojas. La concentración de CNT de la raíz del "Tallow" varió con la etapa fenológica ($P<0.001$), la mayor concentración de carbohidratos ($P<0.05$) ocurrio en la etapa de caída de hojas (60.72%) y la menor durante el desarrollo de hojas (41.11%) y formación de semilla (36.71%). La concentración de CNT de la raíz del "Chinese tallow" se incrementó durante el período de maduración de la semilla hasta la caída de hojas. Si se aplican herbicidas foliares durante el período de translocación de carbohidratos hacia la raíz se puede observar un control efectivo del "Tallow".

Chinese tallow (*Sapium sebiferum* L. Roxb), is a deciduous woody tree that was introduced into the United States in the mid to late 1800s (Scheld et al. 1984, Bruce 1993, Bruce et al. 1997). Tallow has since invaded much of the southern U. S. along the Atlantic and Gulf Coasts in floodplain forests, freshwater wetland basins, coastal prairie, abandoned rice fields, mixed bottomland hardwood forests, as well as disturbed sites (Hunt 1947, Russell et al. 1969, Cameron and LaPoint 1978, Scheld and Cowles 1981, Scheld et al. 1984, Jones and McLeod 1990, Bruce 1993, Jones 1993, Jubinsky 1994, Bruce et al. 1997). Due to the severity of the invasion (Jones and McLeod 1989, 1990; Bruce 1993, Conner 1994, Jubinsky 1994, Bruce et al. 1997) tallow control (both chemical and mechanical) has begun to receive interest, although results have been inconsistent (Jubinksy 1994). The efficacy of different control techniques on Chinese tallow has been reviewed (Jubinsky 1994, Bruce et al. 1997). Mechanical removal of mature trees may be impractical on a region-wide scale due to (1) extensive woodland sizes, (2) expense in such operations, and (3) tallow's ability to vigorously resprout after physical damage (Scheld and Cowles 1981, Jubinsky 1994, Bruce et al. 1997). Biological control has received some interest, but the expense and difficulty in finding a species specific pathogen on tallow has hindered such efforts (Jubinsky 1994). Foliar- and stump-applied herbicidal treatments have been partially successful, but to date, region-wide herbicidal treatment programs have not been implemented (Jubinsky 1994, Bruce et al. 1997).

Root total nonstructural carbohydrate (TNC) reserve cycling is a fundamental ecophysiological plant process (Glerum 1980, Hopkins 1995). Root TNC levels are often correlated with phenological development and used to make management recommendations for herbicidal control treatments (Coyne and Cook 1970, Wilson et al. 1975, Menke and Trlica 1981, Fick and Sosebee 1983, Sosebee 1983). Using root

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Research was funded in part by the U S. Fish and Wildlife Service, The Nature Conservancy of Texas, Monsanto Chemical Company, and Texas Tech University. This is manuscript T-9-000 of the College of Agricultural Sciences, Texas Tech University.

Manuscript accepted 20 October 1997

TNC patterns for woody plant control differs from past control practices which emphasized either (1) identifying a specific herbicide that would kill any plant or (2) identifying specific calendar dates for herbicidal treatments (Sosebee 1983). Neither approach has been consistently successful for woody plant control on a region-wide scale (Sosebee 1983). By timing foliar herbicidal application with downward TNC translocation, herbicides will be assimilated into the perennating buds and organs, where total plant kill should be observed (Boo and Pettit 1975, Wilson et al. 1975, Brady and Hall 1976, Fick and Sosebee 1983, Sosebee 1983). The objectives of this study were to test the hypothesis that Chinese tallow root TNC levels vary during the annual cycle according to demands of different stages of phenological development and develop Chinese tallow control timing recommendations based on TNC movement and phenological development.

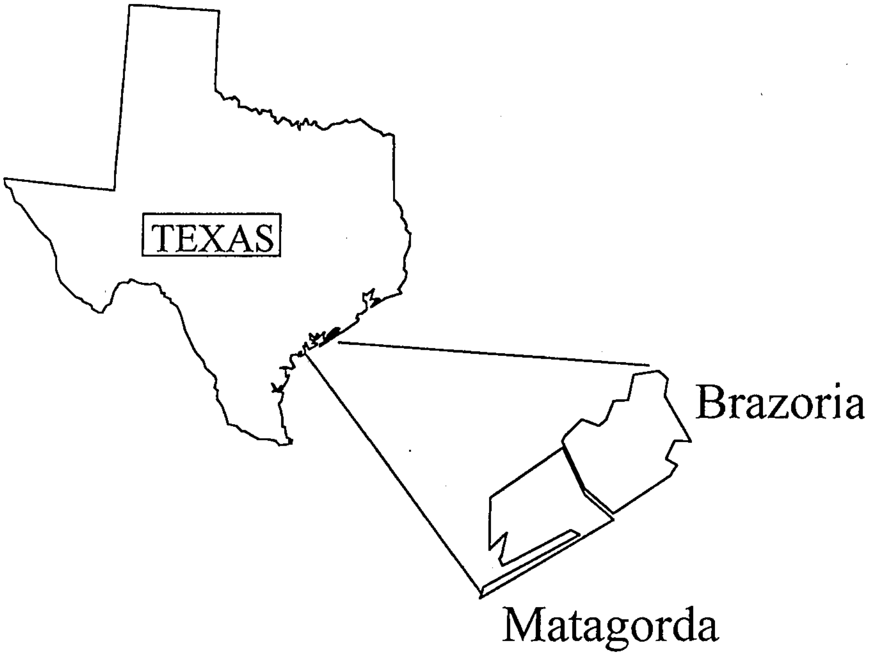

Fig. 1. Location of Chinese tallow study areas along the Texas Coast during 1995 and 1996.

Study Area

This study was conducted along the mid-Texas Coast at The Nature Conservancy of Texas' Mad Island Marsh Preserve (MIMP) (28°6'N 95° 8'W) in Matagorda County and at the Brazoria National Wildlife Refuge (BNWR) (29°10"N 95°8'W) in Brazoria County (Fig. 1). In 1995, a riparian and wetland basin woodland were selected from the MIMP and BNWR, respectively. Both woodlands were dominated by Chinese tallow trees, characterized by high amounts of plant litter on the woodland floor, with ground cover ranging from 45.1 to 64.2% and canopy heights ranging from 9.75 to 11.33 m (Conway 1997). Various sedges (*Carex* spp.) and rushes (*Juncus* spp.) comprised 14.7 to 24.8% and 6.0 to 11.1% of the understory in woodlands at BNWR, respectively, but were infrequently encountered in MIMP. Dewberry (*Rubus trivialis*) was encountered in all woodlands comprising 1.9 to 10.9% of the understory at MIMP but ≤2.5% at BNWR. Chinese tallow seedlings comprised <10% of the understory, but the woodlands had similar amounts of young tallow trees (i.e., number stems >1 cm diameter at breast height [dbh] /m^2), ranging from 0.32 to 0.42 stems /m^2. The woodland at MIMP had more large trees (i.e., number of tallow stems>5 cm dbh]m^2) than at BNWR (Conway 1997).

The mid-Texas coast is coastal prairie, encompassing a region of over 38,000 km^2 It is restricted to a 40–60 km wide band along the coast of the Gulf of Mexico from the Louisiana border to the semi-arid regions of south Texas near Kingsville (Smeins et al. 1992). Diamond and Smeins (1984) described the region as having a mean annual temperature of 20–22°C with a frost free period of 240–320 days. The region is flat, ranging in elevation from 20–75 m (Smeins et al. 1992) with poor drainage. The geology consisted of Beaumont and Montgomery formations, composed of thick beds of sand interspersed with layers of clay and silt (Smeins et al. 1992). Soils of the region consist of dense clay subsoils and are waterlogged during winter, but may exhibit droughty characteristics during dry conditions (Smeins et al. 1992).

Materials and Methods

Root Collection

Chinese tallow roots were collected monthly from November 1995 through October 1996 from the riparian woodland at Mad Island Marsh Preserve (MIMP) and the wetland basin woodland at Brazonia National Wildlife Refuge (BNWR.) These 2 habitats were selected to examine possible differences in tallow root TNC trends among different woodland types. Roots were excavated from the main tap root, below the basal bud zone of 4 randomly selected tallow trees in each woodland during each month (Wilson et al. 1975). Phenological stage of development was recorded for each sample tree. Each tree was inspected for signs of phenological change over the annual cycle. The following phenological stages were recorded as observed: (1) dormancy, (2) bud break, (3) leaf development, (4) seed formation, (5) seed maturation, and (6) leaf fall.

Tallow trees generally have a main tap root with associated lateral roots. Therefore, during root collection, extraneous lateral roots were removed to access the main tap root for sample collection. If the tree was small enough, the entire tap root was removed. If a tree could not be pushed over, a hole was excavated and a section of the main tap root was removed using a pick-axe and shears. Once removed, roots were put into paper bags, and placed on dry ice to prevent enzymatic degradation of TNCs (Boo and Pettit 1975, Wilson et al. 1975). Roots were then placed into a drying oven at 100°C for 1 to 2 hours to halt enzymatic activity (Boo and Pettit 1975, Mounsif 1986). They were then dried at 60–65°C for 1 week to remove any moisture (Boo and Pettit 1975, Sosebee pers. commun.). After drying, roots were ground into a powder using a Wiley mill fitted with a 40 mesh (0.5 mm) screen (Menke and Trlica 1981, Mounsif 1986). Only clean, unblemished root sapwood was used for grinding to prevent contaminating samples with dirt, bark, or other foreign substances (Sosebee, pers. commun.). All root samples were kept in air-tight glass containers until analyzed for TNC.

Root TNC Chemical Analysis

Ground tallow roots were subjected to the anthrone reagent procedure (Yemm and Willis 1956, Mounsif 1986) to determine root TNC concentration (Wan and Sosebee 1990). Individual root samples were divided into 3 subsamples (0.5 g). Each subsample was digested by boiling 60 ml of hydrochloric acid (HCl) in 300 ml flasks for 2 hours (Boo and Pettit 1975, Mounsif 1986). After digestion, samples were cooled and filtered into 100 ml volumetric flasks using Whatman No. 2 filter paper. Once filtered, each flask was brought to volume using distilled water. A 1 ml aliquot was then removed and placed into a 35 ml test tube containing 4 ml of distilled water. The test tube mixture was shaken using a Thermolyne vortex mixer (30 sec). A 1 ml aliquot was then removed from the original test tube and placed into another 35 ml test tube containing 10 ml of anthrone reagent. Test tubes were shaken using the Thermolyne 8 vortex mixer (30 sec). Sample test tubes were then placed into a heater block for 17 mm at 96–100°C, after which they were removed and placed into a cold (22°C) water bath until they reached room temperature. Once at room temperature, samples were analyzed with a Perkin-Elmer Lambda 3B UV/VIS spectrophotometer set at 612 nm, using glucose as the standard. Root TNC concentrations were calculated by dividing the sample spectrophotometric readings by the glucose standard to obtain a percent (%) TNC value on a dry mg/g basis.

Data Analysis

A 2-way analysis of variance (ANOVA) was used to test for overall differences in root TNC concentration (%) between woodland types (i.e., riparian or wetland basin) and among phenological stages (i.e., dormancy, bud break, leaf development, seed formation, seed maturation, and leaf fall). Although roots were collected on a monthly basis, phenological stage of development was the independent variable during analyses to focus on phenological, not monthly variation in root TNC concentrations. Percentage tallow root TNC concentration data were square root transformed (Zar 1996). If differences ($P<0.05$) occurred, least squares mean separation was used to examine differences among phenological stages in root TNC concentrations. However, the means were back-transformed for presentation.

Results

There was no woodland type by phenological stage ($F = 1.30$; 5, 180 df; $P = 0.266$) interaction. There was no woodland type ($F = 1.15$; 1, 180 df; $P = 0.286$) effect (Table 1). Root TNC concentrations varied by phenological stage ($F = 18.65$; 5, 180 df; $P<0.001$). Tallow root TNC concentrations were highest during leaf fall and lowest during leaf and seed development ($P<0.05$).

Discussion

Chinese tallow root TNC trends follow patterns similar to other woody species such as mesquite (*Prosopis glandulosa*), sand-shin oak (*Quercus havardii*), cherry (*Prunus avium*), and poplar clones (*Populus tristis* x *balsamifera*) (Boo and Pettit 1975, Wilson et al. 1975, (Glerum 1980, Isebrands and Nelson 1983, Loescher et al. 1990, Wan and Sosebee 1990). Tallow root TNC levels rapidly decrease during spring when trees break dormancy, buds break, roots grow, and leaves develop. During these periods, roots function as carbohydrate sources, supplying energy to meet increased metabolic costs (*sensu* Hopkins 1995). Tallow root TNC levels continue to decline through the seed formation phase. Once tallow seeds begin to ripen and mature, root TNC levels increase. These fluctuations in root source/sink dynamics are common in woody deciduous trees, where maximum root TNC levels are generally attained before leaf fall after seed/fruit maturation (Loescher et al. 1990). During dormancy, tallow root TNC levels decline slightly, perhaps to meet maintenance respiration and metabolic demands (*sensu* Wilson et al. 1975, Glerum 1980, Loescher et al. 1990, Kozlowski 1992).

Chinese tallow root TNC levels increase during seed maturation until leaf fall, reaching 52% and 61%, respectively (Table 1). These levels are higher than mesquite root TNC levels during its root replenishment stage (14%) (Wilson et al. 1975). When foliar herbicides were applied to mesquite during this replenishment period, effective plant kill was observed (Wilson et al. 1975). Similarly, if foliar herbicides are applied

Table 1. Chinese tallow root total nonstructural carbohydrate (TNC) levels (%) (mg/g) according to phenological stage of development. Tallow roots (n = 4 at each site) were collected monthly from trees in Matagorda and Brazoria Counties, Tex. from November 1995 through October 1996.

		Overall TNC Levels[1]		Riparian tallow TNC Levels		Wetland tallow TNC Levels	
Phenological Stage	Date	(x)	SE	(x)	SE	(x)	SE
			(%)		(%)		(%)
Dormancy	Nov 95–Jan 96	47.94B	1.14	44.15	1.42	51.72	1.52
Bud Break	Feb 96	47.30B	2.32	46.89	3.98	47.72	2.68
Leaf Development	Mar–Apr 96	41.11C	1.24	41.44	1.96	40.79	1.63
Seed Formation	May—Jun 96	36.71C	1.35	36.29	2.03	37.13	1.85
Seed Maturation	Jul–Aug 96	51.69B	2.56	51.82	3.97	51.56	3.37
Leaf Fall	Sept–Oct 96	60.72A	1.53	60.51	2.60	60.94	1.82

[1] Means followed by the same letter are not different ($P>0.05$). Overall TNC levels are data combined for riparian and wetland basin tallow woodlands.

to tallow during its replenishment period, when roots function as carbohydrate sinks, total plant kill should be observed. Phenological development in tallow should be relatively consistent among years (although timing may vary by locale) (Sosebee 1983), therefore, effective tallow control programs may be implemented on a region-wide basis. This is a plausible and attainable goal, where tree mortality has been observed in other woody plant species (i.e., mesquite, sand-shin oak, etc.) when foliar herbicide application was based on phenological development, coinciding with root TNC level increases (Boo and Pettit 1975, Wilson et al. 1975, Wan and Sosebee 1990).

Although mechanical treatment (i.e., shredding, mowing, etc.) of Chinese tallow has had relatively limited success due to tallow's ability to resprout after stem damage (Jubinsky 1994), these data also may be used to time such treatments. Contrary to herbicidal applications, where treatment should coincide with root TNC replenishment, mechanical control should coincide with lowest root TNC concentration. If mechanical treatment coincides with tallow's seed formation stage (i.e., period of lowest root TNC levels) a higher degree of control should be observed more than at other times of the year (Table 1).

This study provides a first step toward Chinese tallow control and management. These root TNC data can be used to time treatments (herbicidal and mechanical) on a region-wide level; from Texas to Florida into North Carolina, regardless of tallow woodland type (i.e., riparian or wetland basin woodland). Unfortunately, these data provide a post-hoc approach to tallow management. Prescribed burning, a proper rotational grazing scheme, and other such land management practices should be used to prevent tallow establishment in areas where it is presently absent or in low densities. Finally, land managers must have a plan to keep tallow out of treated areas or benefits will be short-lived.

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Book Reviews

Holistic Managcmcnt: A New Framework for Decision Making. Second Edition. By Allan Savory with Jody Butterfield. 1999. Island Press, Washington, D.C. [www.island press.org]. 616 p. US$50.00 cloth, US$30.00 paper. ISBN 1-55963-487-1, cloth, ISBN 1-55963-488-X paper.

When Allan Savory brought his ideas and new paradigms on animal arid land management to North America in the 1970's, the range management profession was forced to re-examine long-held beliefs and philosophies. Few concepts, before or since, have divided people into opposing groups with so many strong feelings and differences in thought. His observations proved to be difficult to study by reductionist science and were so unique and so forthrightly advanced that a war of words between the different camps has continued for years. There were successes and failures by practitioners and scientists as the ideas were tried, adapted, and changed. The issues are still debated but much of the rhetoric has ceased as the concepts have matured. Over time the system evolved from the "Savory Grazing Method", with which it became so closely associated in the early 1980's that the names were interchangeable, to a management system as outlined in the 1988 book, *Holistic Resource Management.*

The decade between the first and the present editions of the book witnessed much trial and error implementation and strengthening and clarifying of concepts. "Holistic Resource Management" has now matured into "Holistic Management", a decision-making framework to meet goals while enhancing environmental sustainability. In the present volume, Savory and Butterfield emphasize the management processes of holistic goal setting and the feedback loop of planning- monitoring-controlling-replanning. The thesis is that Holistic Management has broader implications as a process or procedure that can be used in a variety of management situations—not just in natural resource management—thus the change in name.

Holistic Management is divided into 11 parts with 51 chapters and is generally organized around Savory's 4 "key insights" or paradigms and the Holistic Management model. As proposed, the 4 basic "insights" are the foundation for developing any holistic strategy. The first is that one cannot manage only parts of a system without affecting other parts—often negatively. The "whole" is greater than the sum of it's parts and must be considered and managed accordingly. As many of the myriad reactions to a treatment as possible need to be considered in decision-making. This, of course, is similar to the basis of much of the current thought pertaining to ecosystem management. The second basic concept is that environments can be classified on a continuum from "brittle" to "non-brittle" based upon how annual humidity is distributed, how quickly dead vegetation decomposes and what agents cause it (biological vs. weathering), and how that environment responds to treatments. An analysis of environments on this basis indicates that the evidence is quite convincing.

The third basic concept is "time". It is argued that stocking rate is not as important as the length of time livestock are allowed to graze an area. A balance must be achieved between numbers and time so that all forage plants can be grazed once but not re-grazed before it has had a chance to grow.

The fourth point is probably the most controversial and has caused the most divisions among managers, practitioners, scientists, and others in the profession—that of "herd effect" and animal impact. Savory asserts that the excited behavior of bunched herding animals (as in response to predators) has different impacts on the land than the contented, selective grazing of many grazing strategies. Aspects of this contention are also convincing but many questions remain as to it's complete validity. All 4 of these concepts are integrated in holistic management strategies. Separate chapters are devoted to the development of each and discussions concerning tools and discussions in later chapters often relate back to them.

The Holistic Management model defines the "whole" to be managed as the decision-makers, the resource base, and the financial base. This "whole" is then managed to achieve a three-part goal (e.g. quality of life, forms of production, and future resource base) that is the basis for all decision-making. Tools and options are selected that will enhance the ecosystem processes of community dynamics, energy flow, nutrient movement, and water cycling. All decisions are then tested against 8 separate guidelines. The results of following this framework is a planning process for financial, landscape, and grazing components with a feedback loop for monitoring, control, and replanning. Details for each component in the process are also discussed in separate chapters.

Overall, Savory presents a carefully reasoned approach to the discussion of Holistic Management. He devotes space and detail to the background on how concepts evolved through observations, experimentation, and trial and error. At the same time the rhetoric so characteristic of the first edition is low key—there are few direct attacks on "conventional thinking" for example. Presentation of materials is generally well balanced. But one problem area is that, despite exhortations that no tool should be rejected unless it fails testing guidelines, negative impacts of some tools (e.g. fire) are emphasized to a high degree whereas positive aspects are barely mentioned. This leaves an overall impression that the tool has largely negative connotations. Overall, however, this book presents the Holistic Management ideas in a clear and coherent (if not concise— the volume is 620 page long) manner.

There are no literature citations in the text although a few references are mentioned and quoted as appropriate. There is a chapter near the end of the book that discusses pertinent literature for each chapter topic and recommends specific papers and books for further reading. The scope of these suggested readings is varied and fairly complete and, as might be expected, generally support Holistic Management concepts. Another chapter contains notes and background readings for each chapter topic and is helpful in understanding each issue and concept.

Sustainable resource management must consider environmental, social, and economic impacts in the decision-making process. This is the framework presented in *Holistic Management* and the process has a sound business and ecological basis that should be workable in most natural resource situations. Since most of the material in the book discusses land resource management with examples of wildlife and livestock enterprises, it is a valuable and thought-provoking process for land managers to study. The process can then be adapted to their own situations. Managers should critically study and analyze the more controversial aspects of Holistic Management (e.g. herd effect) and forget earlier dicta such as "immediately double your stocking above recommended stocking rates". Such study will enhance the understanding of the many impacts of decisions on all aspects of the "whole" system to be managed. It may be improbable to apply all of the Holistic

Management process to a factory, a household, or a corporation, but for anyone involved with land management and stewardship this book is a valuable guide for decision-making and for developing management strategies. It should be read by natural resource managers and other professionals, including academics, to better understand Holistic Management and it's applicability to ecosystem management.—*C. Wayne Hanselka*, Texas Agricultural Extension Service, Corpus Christi, Texas.

Measuring and Monitoring Plant Populations. By C.L. Elzinga, D.W. Salzer and J.W. Willoughby. 1999. Bureau of Land Management, National Business Center, BC-650B, P.O. Box 25047, Denver, CO 80225-0047. 492 p. Free publication, paper.

This book grew out of workshops on single-species plant monitoring that have been offered jointly by the Bureau of Land Management, the U.S. Forest Service and The Nature Conservancy. The author's many years of experience in plant monitoring are evident throughout the volume. It contains important information that one does not find in standard texts on field biology, statistics or experimental design.

The book includes 13 chapters plus 19 appendices. The introductory chapter emphasizes that monitoring must be tied to management objectives if it is to have much value for land managers. The authors compare and contrast monitoring to related data-collections activities including research, natural history study, implementation monitoring, and ecological measuring change. The second chapter presents 7 steps of the plant monitoring process. One of the strengths of the book appears in this chapter, namely, the importance of doing certain tasks that many readers might take for granted or the importance of conducting a pilot study to field-test one's study design. The remaining chapters deal each of the monitoring steps in detail.

The third chapter deals with factors to consider when setting priorities and selecting the scale and intensity of monitoring. The chapter highlights the differing agendas of researchers and land managers that often lead to different monitoring designs. This is probably one of the least-appreciated and most neglected aspects of monitoring. Chapter 4 covers management objectives, with many examples of complete and confusing management objectives. The authors promote the idea of management implications, a statement of what will happen if the management objective is not met. A commitment to a course of action that will occur if the management objective is not met will increase the likelihood of that action actually being implemented. In Chapter 5, the authors skillfully use examples from artificial populations to illustrate basic principles of sampling. They also use computer simulations to good advantage. The finite population correction factor has generally been ignored in monitoring, but the authors show how it can help increase the precision of estimates of statistical parameters or reduce sample size in certain monitoring designs. There is a clear presentation of type 1 and type 2 errors (false-change and missed-change errors, respectively). Type 2 errors have been neglected by researchers (and therefore not taught to students who become land managers) until recently, but it is crticial for determining the power of statistical tests. Chapter 6 discusses sampling objectives, another subject that has not been treated thoroughly by standard texts. A sampling objective states the desired level of precision, acceptable false- and missed-change error rates, and the magnitude of change one is trying to detect. Failure to develop sampling objectives is probably the main reason why many monitoring studies end up being worthless because they produce equivocal data. Chapter 7 discusses sampling design using data from artificial populations and computer simulations show why the traditional 1m by 1m quadrat is often far inferior to long, narrow quadrats for plant monitoring, a consequence of the fact that most plant populations are clumped.

Chapter 8 covers field techniques for monitoring, including many practical points such as density being a poor measure for long-lived plants that respond to stress by reducing biomass or cover rather than dying. Chapter 9 discusses data collection and management, something that is usually ignored in textbooks, and includes many useful tips on data sheet layout and organization. Chapter 10 explains communication and monitoring plans, topics that savvy land managers will read and take to heart. Chapter 11 presents statistics that resource managers need to know to estimate statistical parameters and conduct statistical tests. The clear presentation on the value of using permanent quadrats will motivate more land managers to use permanent rather than temporary sampling units. The authors discuss statistical programs useful for monitoring, including freeware and shareware. Chapter 12 introduces demography, a monitoring approach that is popular with researchers (who publish papers in journals) but has major limitations for land managers (who have many plant species to monitor). As in previous chapters, there are many practical suggestions for persons considering demographic studies. The subject of the last chapter, completing monitoring and reporting results, is rarely treated in textbooks. It contains a list of topics that should be included in a monitoring report, and will motivate busy resource specialists to assess and report their monitoring results.

The appendices are packed with valuable information dealing with topics such as common monitoring problems, examples of monitoring objectives, selecting random samples, sample size estimation, examples of more complicated sampling designs and formulas, comparisons of vegetation measures for monitoring, and a check list of field equipment. Also included are a table of random numbers and critical values of the t and the chi-square statistic.

The main complaint I have about the book is its rather flimsy binding. The binding on my copy began to fail during my first reading of the book. Nonetheless, *Measuring and Monitoring Plant Populations* fills a major unmet need for resource managers who monitor plants, such as rare species or noxious weeds. This is a very practical yet rigorous treament of plant monitoring. It is a must read for anyone who will be conducting plant monitoring projects.–*Alan T. Carpenter*, Boulder, Colorado.

INSTRUCTIONS FOR AUTHORS (from revised *Handbook and Style Manual*)

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