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Feature Article
Viewpoint: Benefits and impacts of wildlife water developments

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Abstract

Resource managers in the western United States have long assumed that water was a key limiting factor on wildlife populations in arid habitats. Beginning in the 1940s–1950s, state and federal resource management agencies initiated water development programs intended to benefit game species and other wildlife. At least 5,859 such developments have been built in 11 western states. Most state wildlife management agencies in the western United States have ongoing wildlife water development programs that vary greatly in extent. Ranchers and range managers also have developed water sources for livestock, many of which also are used by wildlife. Recently, critics have suggested that wildlife water developments have not yielded expected benefits, and may negatively impact wildlife by increasing predation, competition, and disease transmission. Based upon a comprehensive review of scientific literature, we conclude that wildlife water developments have likely benefitted many game and non-game species, but not all water development projects have yielded expected increases in animal distribution and abundance. Hypothesized negative impacts of water developments on wildlife are not supported by data and remain largely speculative. However, our understanding of both positive and negative effects of wildlife water developments is incomplete, because of design limitations of previous research. Long-term, experimental studies are needed to address unanswered questions concerning the efficacy and ecological effects of water developments. We also recommend that resource managers apply more rigorous planning criteria to new developments, and expand monitoring efforts associated with water development programs.

Key Words: wildlife management, water requirements, stock-tanks, catchments, guzzlers, tinajas.

Resumen

Administradores de recursos en el oeste de los Estados Unidos han por mucho tiempo supuesto que el agua era el principal factor limitante de poblaciones de vida silvestre en hábitats áridos. Empezando en los 1940s–1950s, agencias federales y estatales que manejan recursos naturales iniciaron programas para el desarrollo de aguas construidas, con el objeto de beneficiar a los animales de caza y a otra vida silvestre. Por lo menos 5,859 desarrollos de este tipo han sido construidos en 11 estados occidentales. La mayoría de agencias estatales que manejan vida silvestre en el oeste de los Estados Unidos tienen programas para el desarrollo de aguas construidas. Estos programas varían mucho en magnitúd. Rancheros y administradores de pastizales también han desarrollado aguas contruidas para el ganado, muchas de las cuales son usadas por la vida silvestre. Recientemente, críticos han sugerido que las aguas construidas para la vida silvestre no han rendido los beneficios anticipados y que estos desarrollos pueden hacer daño a la vida silvestre debido al aumento en predación, competencia y transmisión de enfermedades. A base de una búsqueda comprensiva de la literatura científica, concluimos que las aguas construidas para la vida silvestre probablemente sí han beneficiado a muchos animales de caza y a otra vida silvestre, pero no todos los proyectos de desarrollo de aguas construidas han rendido aumentos anticipados en distribución y abundancia de animales. Los efectos hipotizados negativos de aguas construidas en la vida silvestre no son soportadas por datos y permancen altamente especulativos. Sin embargo, nuestro entendimiento de los efectos positivos y negativos de aguas construidas es incompleto, debido a las limitaciones en el diseño de investigaciones previas. Investigaciones a largo plazo, experimentales hacen falta para responder a preguntas sobre la eficacia y los efectos ecológicos de las aguas construidas. También recomendamos que los administradores de recursos apliquen criterios de planificación mas rigurosos a los desarrollos nuevos, y que aumenten esfuerzos de monitoreo asociados con programas para el desarrollo de aguas construidas.

Historical and Current Use of Wildlife Water Developments

In the landmark text *Game Management*, Leopold (1933) articulated 3 fundamental needs of free-ranging wildlife: food,

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water, and cover. Since then, the importance of water to wildlife populations has been considered axiomatic. In arid habitats, the scarcity of free-standing water has long been considered a limiting factor for many game species (Roberts 1977). Since the 1940s–1950s, wildlife managers in the western U.S. have expended considerable effort to enhance existing water supplies and develop new water sources for wildlife.

Wildlife water development programs have evolved over time. Early wildlife water developments were intended to benefit upland game birds or ungulates (Glading 1947, Wright 1959). More recently, water development projects have been used to mitigate the loss of naturally-occurring water sources (deVos et al. 1983) and were designed to provide water for a variety of game and nongame species (Sanchez and Haderlie 1990). Broyles (1998) noted that water development projects also provide social, political, and public relations opportunities for resource managers, sportsmen, and user groups.

Development of water supplies also has been an integral part of livestock and range management throughout the arid West (Vallentine 1980). Quantitative information on the number of water developments built for livestock is difficult to obtain; however, livestock water developments outnumber those constructed solely for wildlife. Many livestock waters are used by wildlife, however, the benefits of these facilities to wildlife have been questioned (Scott 1998).

Four primary types of water developments have been constructed in the western U.S., modified natural tanks, artificial catchments, developed springs, and wells. Natural rock tanks (tinajas) that collect precipitation and surface runoff have been modified to increase interception and storage capacity (Werner 1984). Artificial catchments include earthen reservoirs (Halloran and Deming 1958); concrete dams (Halloran and Deming 1958); sand dams (Bleich and Weaver 1983); adits (Parry 1972); and units that incorporate a precipitation collection surface, storage tank, and drinker (Gunn 1990). Existing springs have been developed to increase water flow and availability (Bleich et al. 1982). Horizontal and vertical wells have been used where other types of developments were not practical (Kindschy 1996).

Most western U.S. state wildlife agencies have used water developments as a wildlife management tool; however, the extent of water development programs varied (Table 1). California, Arizona, Nevada, and Oregon had the largest historical and current water development programs, measured by numbers of facilities and expenditures for construction and maintenance. However, agency expenditures on water developments were difficult to estimate, because many projects were built and maintained using donated labor and materials. Water developments also have been built by federal land management agencies such as the USDI Bureau of Land Management (USDI Bureau of Land Management 1964) and USDA Forest Service (Quigley et al. 1989); however, we were unable to obtain region-wide data on these projects.

The Controversy

For many years, the need for water developments in arid habitats was unquestioned, and such developments were assumed beneficial to game and nongame wildlife species. Contemporary resource management references recommend development of new water sources to benefit ungulates and other wildlife (e.g., Kie et al. 1994, Kindschy 1996).

Recently, wildlife water developments have received critical scrutiny. Resource managers have questioned the need for continued development of new water sources (Sanchez and Haderlie 1990). Critics of wildlife water developments have suggested that establishment of new water supplies in arid habitats may not yield expected benefits, and can have adverse impacts (Broyles 1995, Brown 1998). Economic costs and benefits of wildlife water developments also have been challenged (Broyles 1998).

Wildlife Responses to Water Developments

The underlying assumption of water development programs has been that the scarcity of surface water in arid habitats was a primary factor limiting wildlife populations. Managers anticipated that provision of additional water sources would benefit wildlife populations; by expanding animal distribution, increasing productivity, reducing mortality, and increasing fitness. Here, we present our perspective on the effects of water developments on game and non-game wildlife; derived from an extensive literature review and discussions with resource managers throughout the western U.S.

Game Species

Upland Game Birds

Many early water developments were built for quail; however, the impacts of these facilities on quail populations vary. Gambel's quail (*Callipepla gambellii* Gambel) and scaled quail (*Callipepla squamata* Vigors) can meet most of their water needs by consuming succulent foods (Hungerford 1960, Schemnitz 1994). However, Leopold (1977:183) indicated that desert quail required drinking water to survive periods of sustained heat and drought. Desert quail frequently drank from catchments, particularly during hot and

Table 1. Current wildlife water development programs of 11 western U.S. state wildlife agencies. Information obtained from mail and telephone survey conducted October–December 1997 (Arizona Game and Fish Dept., unpublished).

State	No. developments[1]	Ongoing program	Annual expenditures[2]
Arizona	840	yes	$755,000
California	2,500	yes	data unavailable
Colorado	data unavailable	no	data unavailable
Idaho	data unavailable	yes	data unavailable
New Mexico	43	yes	$50,000
Nevada	1,000[3]	yes	up to $110,000
Oregon	1,000	yes	$75,000-100,000
Texas	135	yes	$11,000
Utah	250	yes	$50,000
Washington	6	yes	outside donations only
Wyoming	85	yes	$14,000

[1]Number of developments historically constructed or currently maintained.
[2]Recent expenditures. Because detailed expenditure records often were unavailable, most figures are rough estimates.
[3]Includes developments built by other resource management agencies.

dry periods (Elder 1956). Early studies reported that water developments increased quail distribution and abundance (Rahm 1938, Wright 1953). Subsequent research suggested that in some areas, water developments did not substantially increase quail populations or hunter success (Hungerford 1960, Webb and Gallizioli 1963), and were not economically justifiable if constructed for quail alone (Campbell 1961). We concur with Campbell's (1961) suggestion that climatic factors accounted for regional differences in quail use of water catchments, and that these developments were most beneficial in areas characterized by drought during the spring-summer breeding season.

Chukar partridge (*Alectoris chukar* Gray) have been introduced into many arid upland regions of the western U.S., a process enhanced by development of new water sources. In Nevada, installation of guzzlers increased existing chukar populations, facilitated establishment of new populations, and improved hunter distribution and hunt success (Benolkin 1990).

Surface water is required by mourning doves (*Zenaida macroura* L.) and white-winged doves (*Zenaida asiatica* L.), consequently both species likely have benefitted from water developments in arid habitats. Mourning and white-winged doves frequently used water catchments in Arizona (Elder 1956). In Idaho, movements and habitat use of radio-tagged mourning doves suggested that dove populations could be increased by establishing new permanent waters, where distances between existing watering sites were >6 km (Howe and Flake 1988).

Availability of free-standing water appears to be an essential habitat component for Merriam's turkey (*Meleagris gallopavo merriami* L.). In Arizona, turkey population increases were associated with construction of wildlife water developments (Shaw and Mollohan 1992). We concur with current management guidelines recommending that water sources be available within each 2.59 km^2 of suitable turkey habitat (Hoffman et al. 1993).

Waterfowl

Earthen tanks can provide valuable habitat for migrating and nesting waterfowl. Cutler (1996) observed 6 species of migrant waterfowl using earthen tanks in Arizona. Nesting habitat suitability of man-made ponds is strongly influenced by water surface area and characteristics of emergent and bank vegetation (Lokemoen 1973, Rumble and Flake 1983). We note that the habitat potential of many stocktanks in the western U.S. has not been realized because of a lack of vegetative cover (Menasco 1986, Scott 1998).

Desert Bighorn

Water is considered a key habitat requirement of desert bighorn (*Ovis canadensis* Shaw) (McCarty and Bailey 1994). Desert bighorn readily use surface water; however, populations of desert bighorn persist in areas where free water is lacking on a seasonal or permanent basis (Krausman and Etchberger 1996). These sheep apparently obtain sufficient water from cacti and other succulent forage items (Warrick and Krausman 1989).

Habitat use by desert bighorn often is positively correlated with proximity to water sources, including water developments. In 6 studies reviewed by McCarty and Bailey (1994), sheep most often were observed within 0.4–3.2 km of a water source. Significant preferences for areas closer to water have been found during hot, dry periods (Wakeling and Miller 1989). Waterholes also may serve as focal areas for social interactions among sheep (Olech 1979). However, in some desert sheep populations, habitat use appears not to be constrained by the distribution of water sources (Krausman and Leopold 1986a, Krausman and Etchberger 1995).

Water developments have been a centerpiece of desert sheep habitat management throughout the arid West. Use of water developments by desert bighorn is well documented (Graves 1961, Campbell and Remington 1979), but some catchments intended to benefit sheep have received little or no use (Krausman and Etchberger 1995). Bighorn populations have increased after development of new waters (Leslie and Douglas 1979), or declined in response to drying of natural springs (Douglas 1988). However, some authors have argued that desert sheep populations may not benefit from water developments (Broyles 1995, Krausman and Etchberger 1996). We believe that water developments have benefitted some, but not all populations of desert bighorn.

Elk

Elk (*Cervus elaphus* L.) are primarily associated with mesic forest habitats, where water generally is not a limiting factor (Boyd 1980:22). In arid habitats, habitat use by elk is strongly affected by availability of surface water; areas within 0.4–1.6 km of water sources are used most heavily, particularly in dry periods or during lactation (Delgiudice and Rodiek 1984, McCorquodale et al. 1986, Biggs et al. 1997). Close proximity to water (within 0.4–0.8 km) was characteristic of elk calving areas in Arizona (Brown 1994).

Over the last 20 years, elk populations have expanded dramatically in arid shrubsteppe, woodland, and forest habitats of the western U.S. We contend that water developments have played a major role in this expansion. Scarcity of water likely limited prior elk use of these areas, because of the high water requirements of female elk during lactation (Skovlin 1982).

Mule Deer

Mule deer (*Odocoileus hemionus* Rafinesque) in arid regions are dependent upon free water (Wolfe 1978:367). Mule deer typically are found in close proximity to water sources, particularly during dry periods (Rautenstrauch and Krausman 1989a, Boroski and Mossman 1996). In Arizona, water developments received heavy use by desert mule deer, primarily during hot summer months (Remington et al. 1984, Hervert and Krausman 1986). Does visiting catchments consumed more water than did males, perhaps due to increased water requirements associated with lactation (Hazam and Krausman 1988). An apparent dependence of some desert mule deer on water catchments has been demonstrated experimentally (Hervert and Krausman 1986).

There is good evidence that water developments have benefitted mule deer in arid Southwestern habitats. Seasonal desert mule deer ranges in Arizona were occupied year-long after construction of water developments (Wright 1959). Provision of new water sources also increased deer densities in habitats where water previously had been limiting (Bellantoni et al. 1993). deVos and Clarkson (1990) found a positive relationship between mule deer harvest and the number of water developments built over an 11-year period. Deer numbers increased during a 5-year period following development of wildlife waters in New Mexico (Wood et al. 1970).

White-tailed Deer

Surface water is an essential habitat component for white-tailed deer (*Odocoileus virginianus* Zimmerman) in arid habitats. Habitat use by white-tailed deer in the Southwest is closely tied to the availability of free-standing water (Maghini and Smith 1990).

Water developments have likely benefitted white-tailed deer populations in the Southwest. White-tailed deer regularly visited water developments, particularly during hot-dry seasons (Maghini and Smith 1990). In Arizona, Coues white-tailed deer strongly selected areas within <0.4 km of artificial and natural water sources, avoiding areas >1.2 km away. Availability of supplemental water may increase fawn survival and recruitment when forage moisture is low (Ockenfels et al. 1991).

Pronghorn

The importance of surface water to pronghorn (*Antilocapra americana* Ord) remains a source of debate (Yoakum 1994, Hervert et al. 1998). However, high density pronghorn populations usually occur in habitats with abundant free water, whereas habitats with few water sources support low pronghorn densities (Yoakum 1994). Hervert (1996) observed that Sonoran pronghorn herds that utilized surface water were larger than herds that did not. In some areas, habitat use by pronghorn is related to the availability of surface water. When forage moisture content was lowest, Wyoming pronghorn were found within 4.8–6.4 km of water (Sundstrom 1968, Boyle and Alldredge 1981). In Arizona, pronghorn fawns selected bed sites within 0.4–0.8 km of water, avoiding areas >1.2 km away (Ticer and Miller 1994). In New Mexico, yearling pronghorn remained closer to water than adults (Clemente et al. 1995). Sonoran pronghorn in Arizona and Mexico were located closer to water than expected by chance (Wright and deVos 1986). Other studies have reported that availability of water did not influence habitat use by adult pronghorn (Hughes and Smith 1990, Deblinger and Alldredge 1991, Ockenfels et al. 1994).

Water developments have been a popular habitat improvement technique for pronghorn, and these developments often receive heavy use when succulent forage is unavailable (O'Gara and Yoakum 1992, Yoakum 1994). Water developments may improve pronghorn distribution in some situations (Beale and Smith 1970, Heady and Bartolome 1977). However, we concur with Deblinger and Alldredge (1991), who cautioned that water developments were not the sole determinant of pronghorn distribution or density.

Mammalian Predators

The literature is equivocal concerning the dependence of mammalain predators on free water. Most can obtain needed moisture from their prey, if additional water is not required for thermoregulation (Schmidt-Nielsen 1964). Some species, e.g., ringtails (*Bassariscus astutus* Lichtenstein) and kit foxes (*Vulpes macrotis* Merriam) are believed not to require free water (Chevalier 1984, Golightly and Omart 1984). However, there are many anecdotal observations of mammalian predators drinking from natural or human-made water sources (Ballard et al. 1998).

There is evidence that water developments attract mammalian predators; however, the effects of these facilities on predator populations are unknown. Cutler (1996) observed 6 species at water developments in Arizona (kit fox, gray fox [*Urocyon cinereoargenteus* Baird], badger [*Taxidea taxis* Schreber], coyote [*Canis latrans* Say], bobcat *Lynx rufus* Schreber], and mountain lion [*Felis concolo*r L.]). Predator observations and sign also were greater at water developments compared to unwatered control sites (Schmidt and DeStefano 1996). In contrast, Smith and Henry (1985) found no difference in predator use at water developments and unwatered control plots.

Non-Game Species

Small Mammals

Terrestrial small mammals found in arid habitats have physiological and behavioral adaptations that minimize or eliminate the need for free water (Mares 1983); consequently these species are relatively unaffected by development of new water sources. In Arizona, water developments had little or no influence on lagomorphs and rodents (Smith and Henry 1985, Cutler 1996). However, in New Mexico, small mammals were more abundant at water units compared to unwatered comparison plots, a difference attributed to development-related debris and habitat alteration (Burkett and Thompson 1994).

Unlike other small mammals, bats are strongly attracted to water sources in arid habitats. Water catchments are used for drinking, and serve as foraging areas for insectivorous bats (Kuenzi and Morrison 1997). In Arizona, 7–9 species of bats were captured at earthen tanks and other water developments (Cockrum 1981, Cutler 1996). Similarly, bat activity was higher at water developments than at unwatered control sites (Schmidt and DeStefano 1996). Because some bat species are dependent upon surface water (Schmidt and Dalton 1995), water developments likely have expanded bat distribution, particularly in areas where suitable roosts are present (Geluso 1978).

Birds

Birds living in arid environments vary greatly in their dependence on free water (Dawson and Bartholomew 1968). Nevertheless, water developments are heavily used by many bird species, including passerines, shorebirds, waterfowl, and raptors. Gubanich and Panik (1986) observed 40–44 species using waterholes in Nevada. Availability of water affected bird distribution during Summer and Fall dry periods, and a number of species appeared to be "water-dependent." In Arizona, 150 bird species occurred at or near wildlife water developments, 60 of which were observed drinking water (Cutler 1996). Because bird use peaks during spring and fall migration periods, water developments and associated vegetation "oases" may be important stopover sites for migratory species.

Water developments and associated vegetation provide food, water, and nesting habitat for breeding birds; however, the net effects of these developments on breeding birds vary. In Arizona, total bird abundance and species richness were negatively correlated with distance from wildlife water catchments at 1 of 2 study sites (Cutler 1996). Other studies in Arizona and New Mexico found no difference in species richness or abundance at water developments compared to unwatered control plots (Smith and Henry 1985, Burkett and Thompson 1994).

Raptors appear to benefit from water developments, particularly in desert habitats. Developments and associated structures or vegetation provide water for drinking and bathing, perches, nest substrates, and foraging areas with concentrations of potential prey (Kochert et al. 1988, Cutler 1996). In Arizona and New Mexico, raptor sign was more abundant at water developments than at unwatered control plots (Burkett and Thompson 1994, Schmidt and DeStefano 1996). Mesquite trees (*Prosopis glandulosa* Torr.) established at stocktanks provided roosting, nesting, and winter habitat for long-eared owls (*Asio otus* L.) (Kochert et al. 1988, Cutler 1996). Harris' hawks (*Parabuteo unicinctus* Temminck) require free water during the breeding season; water developments have allowed population expansion into previously unoccupied Sonoran desert habitats (Dawson and Mannan 1991).

Herpetofauna

Many reptiles found in arid habitats will drink water when it is available; however, most species are believed not to require free water (Mayhew 1968). Studies in the southwestern U.S. generally have reported that water developments did not affect reptile abundance or species richness (Smith and Henry 1985, Cutler 1996). However, in New Mexico, snakes and lizards were more abundant at watered sites, a difference attributed to the presence of development-related debris (Burkett and Thompson 1994). One snake species found in the southwestern U.S., the wandering garter snake (*Thamnophis elegans* Baird and Gerard), opportunistically inhabits aquatic habitat provided by stocktanks (J. Howland, Ariz. Game and Fish Dept., pers. comm.).

In the Southwest, earthen tanks and other water developments provide extremely valuable habitat for amphibians. Stocktanks in New Mexico supported breeding populations of 5 toad species that also occurred on a nearby, intermittently flooded playa (Cruesere and Whitford 1976). In Arizona, Jones (1988) found 8 amphibian species that occurred only in stocktanks and other permanent surface waters. Studies in Arizona and New Mexico found 2–4 species of amphibians at water developments, species that were absent on unwatered control plots (Smith and Henry 1985, Burkett and Thompson 1994). In Arizona, one amphibian, the Sonora tiger salamander (*Ambystoma tigrinum stebbinsi* Green) currently is found only in livestock stocktanks (Collins 1998). Stockponds and earthen tanks represent the bulk of occupied habitats for ranid frogs (*Rana* spp) widely extirpated from natural habitats (Rosen et al. 1995, Sredl and Howland 1995). These artificial habitats are managed as refugia and source populations for future frog reintroductions (Rosen and Schwalbe 1998). Sredl and Saylor (1998) found similar reproductive success in frog populations occupying human-made ponds and natural habitats.

Water developments also provide habitat for turtles. In Arizona, Sonoran mud turtles (*Kinosternon sonoriense* LeConte) were considerably more abundant in stocktanks than in stream pools (van Loben Sels et al. 1995). Yellow mud turtles (*K. flavescens* Agassiz) also were commonly found in stocktanks (Menasco 1986).

Adverse Impacts of Wildlife Water Developments

Critics suggest that water developments may adversely affect wildlife expected to benefit from these facilities. Four potential adverse impacts are commonly cited: predation, competition, direct mortality, and health problems resulting from poor water quality or disease transmission. Here, we evaluate the evidence supporting these contentions.

Predation

As reported elsewhere in this paper, avian and mammalian predators are attracted to water developments, leading some to suggest that these facilities may function as "predation sinks." The literature does contain references to predation at natural waterholes or water developments; typically anecdotal observations of individual predation events, inferences based upon indices of predator use, or discoveries of prey remains (Ballard et al. 1998, Cutler 1996). However, data on predator abundance and predation rates at water developments versus unwatered areas are lacking. Consequently, the "predation sink" effect remains an untested hypothesis.

Competition

Several authors have suggested that water developments may exacerbate competition, particularly among native and exotic ungulates. Feral burros (*Equus asinus* L.) are strongly attracted to water developments, where they often deter use by desert bighorn (Weaver 1973). Consequently, many wildlife water developments are fenced to exclude burros and domestic livestock (Brigham 1990). In some areas, water developments have increased abundance of deer and burros, perhaps creating competition with desert bighorn for a limited forage base (Krausman and Leopold 1986b). Because desert bighorn are poor competitors (Geist 1985), such competition could adversely impact sheep populations. We note that the influence of water developments on competitive interactions among wild and domestic ungulates has not been directly studied. Consequently, presumed impacts of increased competition remain an untested hypothesis.

Direct Mortality

Water developments have caused direct mortality of wildlife that become trapped in these facilities. Mortalities of birds and small mammals in livestock troughs and other water facilities have been widely reported (Schemnitz et al. 1998, Scott 1998). Hoover (1995) found desert tortoise (*Gopherus agassizii* Cooper) remains in guzzlers in California. Mule deer and bighorn sheep have died after becoming trapped in earthen tanks and tinajas (Baber 1983, Arizona Game and Fish Dept., unpubl. data). Similar entrapment mortalities also occur in natural water catchments (Halloran and Deming 1958, Mensch 1969). Construction of access and escape ramps can reduce wildlife mortalities in natural and man-made water catchments (Wilson and Hannans 1977, Schemnitz et al. 1998). Detailed studies of wildlife mortality at water developments have not been conducted; however, we suggest that these mortalities are probably negligible from a population perspective. In some situations, water developments may reduce wildlife mortalities. Provision of alternative water sources reduced drowning of mule deer and other ungulates attracted to deep, concrete-lined canals (Rautenstrauch and Krausman 1989b).

Hunters also harvest wildlife at water developments. Species commonly taken at these facilities include: deer, elk, band-tailed pigeon (*Columba fasciata* Say), Merriam's turkey, and waterfowl (S.R., J.D., pers. obs.). Ethical aspects of hunting at water developments have been a source of debate among some sportsmen; however, to our knowledge, adverse biological impacts have not been identified or suggested.

Water Quality

Poor water quality is a significant concern at some water developments; however the impacts on wildlife are largely unknown. In summer, some Arizona catchments contained potentially toxic algae, bacteria, hydrogen sulfide, and ammonia (Kubly 1990, Schmidt and DeStefano 1996). Modification of tinajas to increase storage capacity can prevent flushing during runoff events, and may exacerbate water quality problems (Kubly 1990). Consumption of water-borne toxins has been suggested as a potential explanation for desert sheep mortalities near waterholes, as well as sudden, unexplained sheep dieoffs (deVos and Clarkson 1990, Broyles 1995). However, data supporting these hypotheses are lacking. High levels of dissolved minerals may reduce water quality in some water developments, particularly those fed by groundwater (Kubly 1990). In Wyoming, pronghorn avoided water with >5000 ppm total dissolved solids (O'Gara and Yoakum 1992).

It has been suggested that desert water developments facilitate transmission of wildlife diseases, but there are limited data supporting this contention. We found only 1 documented case of wildlife mortality caused by disease spread from a water development (Swift 1996). In California, desert bighorn lambs drowned in the storage tank of a water catchment, apparently while trying to obtain water. The decomposing carcasses provided a substrate for *Clostridium botulinum* bacteria. Subsequent release of botulinum toxin into the drinker resulted in the deaths of ≥45 sheep. Broyles (1995) speculated that water developments might facilitate spread of *Trichomonas gallinae*, a protozoan parasite that causes avian trichomoniasis. Trichomoniasis outbreaks have occurred in urban areas where birds concentrate at feeders and birdbaths; however, transmission of trichmoniasis via wildlife water developments has not been documented (Arizona Game and Fish Department 1988, Brown 1989:267). A recent study (Hedlund 1996) suggested that water-borne transmission of *Trichomonas* may not be as common as previously thought.

Net Benefits of Wildlife Water Developments

We contend that water developments have benefitted some wildlife populations in arid habitats of the western U.S. Increased availability of surface water has increased the distribution and or abundance of popular and economically important game species such as mule deer, white-tailed deer, elk, chukar, and Merriam's turkey, and has increased opportunities for wildlife observation and harvest. Water developments also benefit nongame wildlife, particularly birds, bats, and amphibians. Perceived negative impacts of water developments on wildlife resulting from predation, competition, direct mortality, and disease are not supported by data and remain largely speculative. However, we recognize that the ecological effects of water developments are poorly understood, and in some cases, expected benefits to game species and other wildlife have not occurred.

Management Implications

Given the high cost of water development construction and maintenance, we believe that resource management agencies should invest more effort in planning, monitoring, and managing these facilities.

In the past, water developments were considered inherently beneficial to wildlife, wherever they were constructed. Following decades of effort by resource managers, we believe that many suitable locations for wildlife water developments have been utilized, and in many areas, scarcity of water no longer limits wildlife populations. Merely adding new water sources to the landscape is no longer adequate justification for new projects. Therefore, we recommend that future wildlife water development projects should: (1) have a solid biological basis, (2) reflect clearly articulated management objectives, and (3) include a formal economic benefit:cost analysis. We also recommend that managers consider options to enhance the habitat value of existing water developments, particularly earthen tanks.

Monitoring is a key component of modern resource management, and in our opinion, an under emphasized element of water development programs. Six of the western U.S. state wildlife agencies we contacted had conducted resource monitoring associated with water developments. Monitoring was typically of limited duration and intensity, and focused on water availability, water quality, and observations of animals visiting these facilities.

We recommend that resource management agencies expand formal monitoring of wildlife water developments. Well-designed monitoring would facilitate data-driven management of water development programs and more efficient use of labor and capital resources. Monitoring efforts should reflect clearly defined management objectives, and use standardized methods to measure resource outputs such as: wildlife distribution, population performance, harvest rates, hunter-days, and hunter success. We also recommend that resource managers conduct regular, site-specific assessments of individual water developments; to decide if they should be maintained in their existing state, modified, abandoned, or removed.

Research Needs and Design Considerations

Despite the tremendous investment in wildlife water developments, there have been few studies examining their ecological effects. Recent studies have furthered our understanding of water development impacts on non-game wildlife; however, most information on the response of game species is anecdotal, observational, or derived from research designed to address other questions. Studies of wildlife water developments frequently have been compromised by 1 or more design weaknesses, including: lack of replication, non-independence of watered and unwatered sampling units, small sample sizes, short study periods, and potential confounding by weather and other effects. In addition, many studies used animal abundance as a response variable, a potentially misleading indicator of habitat quality (VanHorne 1983). Because of these limitations, our knowledge of wildlife water development effects rests on a shaky foundation.

Clearly, there are important, unanswered questions concerning the ecological impacts of water developments, as well as their efficacy in meeting wildlife management objectives. We believe that research on wildlife water developments should be a high priority. Specifically, we suggest that researchers focus on 5 topic areas: (1) effects of water developments on the population performance, distribution, and habitat use of game and non-game wildlife species; (2) effects of water developments on mammalian predator population performance, distribution, habitat use, and predation rates; (3) water quality in catchments versus natural water sources; (4) secondary effects of water developments on adjacent plant communities; and, (5) the role of water developments in transmission of wildlife diseases.

Future studies of water developments need to be long-term, capturing an adequate range of variation in climatic conditions and other temporal phenomena affecting wildlife populations (deVos et al. 1998). In the southwestern U.S., we believe that studies ≥10 years in duration would likely be required to distinguish "natural" variation from treatment effects. Such studies also need to be conducted at a spatial scale appropriate to the research questions and species of interest.

To develop clear cause-and-effect relationships, researchers must experimentally manipulate water developments. We envision 2 general types of experiments, each testing a different hypothesis and management option. The first type of experiment would test effects of water addition, by constructing new water sources in areas previously lacking such developments. The second type would test effects of water removal, by manipulating water availability at existing developments. We acknowledge that attaining true replication of experimental treatments will be difficult or perhaps impossible in some cases. In such circumstances, alternative approaches developed for impact assessment studies, such as the Before-After-Control-Impact-Pairs design (Stewart-Oaten et al. 1986, 1992) could be used.

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Livestock-guarding dogs in Norway Part II: Different working regimes

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Abstract

Livestock-guarding dogs are an effective way of protecting rangeland sheep from predators. However, open mountain/forest range and widely ranging sheep are factors that may make adaptation to Norwegian conditions difficult. This paper focuses on the dogs' working patterns and effectiveness under different working regimes. A 3,500 ha. unfenced forest/mountain range pasture in bear habitat comprised the research area in which 624 sheep from 2 herds grazed. The field trial lasted 3 months, and a total of 10 Great Pyrenees participated for various time intervals. Three different working regimes were evaluated: 1) loose dogs without the command of a dog handler (Method A); 2) loose dogs under the command of a dog handler (Method B); and 3) loose dogs guarding sheep inside a fenced, 1 km^2 forest pasture (Method C). Nocturnal behavioural activity patterns and data on predation were recorded. Method A proved too uncontrolled for Norwegian conditions, because sheep dispersed too widely and dogs ranged too far, causing conflicts in nearby settlements with wildlife, and with livestock. Pasture dogs (C) were >3 times less active and were engaged in guarding activities < 50% as often as patrol dogs (B). However, they barked >15 times more frequently, and no sheep carcasses were found inside the fence. Therefore, Method C probably had the best preventive effect.

Key Words: Great Pyrenees, behavior, sheep, carnivores, depredation

Resumen

Los perros guardianes de ganado son un medio efectivo de proteger los ovinos de los predatores. Sin embargo los pastizales de montaña abierta/bosque y el amplio rango de los ovinos son factores que pueden hacer dificil la adaptación a las condiciones norguegas Este artículo se enfoca en los patrones de trabajo de los perros y su efectividad bajo diferentes regímenes de trabajo. El área de investigación fue un potrero sin cercar de 3,500 ha de pastizal de montaña/bosque en hábitat de osos y en el cual apacentaron 624 borregos divididos en dos rebaños El ensayo de campo duró 3 meses y un total de 10 perros Great Pyrenees participaron en varios intervalos de tiempo. Se evaluaron 3 diferentes regímenes de trabajo 1) perros libres sin la dirección de un perro líder (método A); 2) perros libres bajo el mando de un perro líder (Método B) y 3) perros libres cuidando ovinos dentro de un potrero cercado de 1 km^2 en un área de bosque (método C). Se registraron los patrones de comportamiento de actividades nocturnas y datos de predación. El método A resultó muy sin control para las condiciones noruegas porque los ovinos se dispersaron muy ampliamente y los perros se movieron muy lejos causando confilctos en asentamientos humanos cercanos con la fauna silvestre y el ganado. Los perros guaridanes del método C fueron mas de tres veces menos activos y estuvieron en actividades de guardia menos del 50% de las actividaes de guardia realizadas por los perros patrulleros (método B). Sin embargo, los perros del método C ladraron más de 15 veces mas frecuente y no se encontraron cadáveres dentro de la cerca. Por lo tanto el método C probablemente tiene el mejor efecto preventivo.

More than 100,000 sheep disappear each year on Norwegian mountain and forest ranges during 3 months of summer grazing (Miljøverndepartementet 1997). Depredation caused by protected large carnivores [Scandinavian brown bears (*Ursus arctos*), lynx (*Lynx lynx*), wolves (*Lupus lupus*) and wolverines (*Gulo gulo*)] can exceed 70% of the total losses in severely affected areas (Kvam et al. 1995, Mysterud and Mysterud 1995). The Norwegian Government wants to increase/recover the populations of large carnivores and to maintain a sustainable sheep farming at the same time (Miljøverndepartementet 1997), which means that we need to find preventive attempts to reduce depredation.

Livestock-guarding dogs might be an effective method for protecting sheep from predators (Lorenz and Coppinger 1986, Coppinger et al. 1988; Green and Woodruff 1990, Andelt 1992). A strong social bonding between dog and sheep based on raising the puppy with sheep from the age of 6–8 weeks is recommended to assure a trustworthy, attentive and protective dog (Coppinger et al. 1983; Lorenz and Coppinger 1986, Green and Woodruff 1990, Sims and Dawydiak 1990). However, widely dispersing sheep (herding is not common)

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and open (unfenced), rough ranges make it difficult to use guarding dogs in Norway. Additionally, free public access is guaranteed by law to all rangelands (Lov om friluftslivet 1957), and dogs are not allowed to be loose during the summer in order to protect wildlife (Viltloven 1981), grazing livestock (Bufeloven 1926), and farmed reindeer (Reindriftsloven 1978).

This paper encompasses results on the Great Pyrenees' working patterns and effectiveness under different working regimes. Part I focused on basic behavioral characteristics of the Great Pyrenees (Hansen and Bakken 1999).

Methods

Study Area

The study was conducted in Holandsfjellet, an unfenced grazing area located in the municipality of Lierne in Nord-Trøndelag County, in mid-eastern Norway (Fig. 1). The area chosen for the field trial fulfilled 3 criteria: 1) it was located in occupied bear habitat, with annual predation rates of 10–20% of all sheep released; 2) it represented a traditional Norwegian mountain and forest range, in which the sheep dispersed widely; and 3) it was unfenced and situated close to human settlements, a condition typical of most Norwegian mountain ranges.

Dogs

A total of 10 Great Pyrenees dogs were used. Most of the data are on dogs identified as No. 2 and 3 (2 years old) and No. 6 and 7 (3 years old), which worked continuously the last month of the study. All dogs were reared on sheep farms from the age of 12–16 weeks, but in following strong recommendations from the Norwegian Kennel Club, they were handled by several different people.

Field Trials

The field trials lasted from 7 June until 3 September 1995. A total of 624 sheep (lambs and ewes) from 2 different herds (Herd I and II), were released onto the 3,500 ha. summer pasture. The sheep were not familiar with guarding dogs, and an initial 3-week period was used to familiarize the sheep with the dogs in small paddocks prior to their release onto the open range. The dogs always worked in teams of 2 or 3. Three ways (i.e., "A", "B", and "C") of using guarding dogs at night were evaluated. Because of insurmountable problems encountered with method A, the original procedures were redesigned to include methods B and C.

Method A: Loose dogs in the grazing area without direct supervision of a dog handler.–Six dogs were released from 3 tent camps in the herding area and were allowed to work independently. Radio telemetry was used when the dogs were out of sight. These dogs are referred to as "loose dogs".

Method B: Loose dogs patrolling the herding area under the command of a dog handler.–Dogs No. 2 and 3 were used. They were strongly bonded to the dog handler and did not cause trouble by wandering off. These dogs are called "patrol dogs". Different parts of the herding area were patrolled each night.

Method C: Loose dogs guarding sheep inside a 1 km^2 , enclosed forest pasture, in which 120 sheep grazed.—Dogs No. 6 and 7 were used. A 3-strand, 60-110 cm high electric fence (Ultra Electronic 1600, 50Hz, 3.5 W) surrounded the pasture. Electricity was turned off during the hours that bear depredation was most likely to occur (2300–0600 hrs). The dogs were leashed inside the pasture during the day. These dogs are called "pasture dogs".

Observations

Emphasis was put on documenting the activity patterns of the dogs at night, since most depredation occur during this time. Individual behavior patterns were estimated by scan sampling at 150 sec intervals during two, 30-minute periods each night, representing a total of 1,219 behavioral observations on dog No. 6, 1,218 observations on dog No. 7, 494 on dog No. 2, and 489 on dog No. 3. Sixteen different behaviors were registered, but were finally categorized into 3 behavioral categories: "inactivity" (laying, sitting, standing); "guarding" (patrolling, ranging around, alertness, barking, and scent marking); and "other activities" (walking, running, sniffing, digging, hunting, playing, social interactions, comfort behavior). Distances between the dog and the sheep and between the dog and the observer were recorded as objective measures for the strength of the social bonding between dog-sheep versus dog-man. Behavioral reactions of the dogs towards sheep and wildlife were also recorded. After the grazing season, data on sheep depredation were collected. These were compared to data on neighbouring herds and to data from the previous 3 years.

Statistics

Due to the low number of dogs, descriptive statistics were applied for most of the data. When valid, SAS pro-

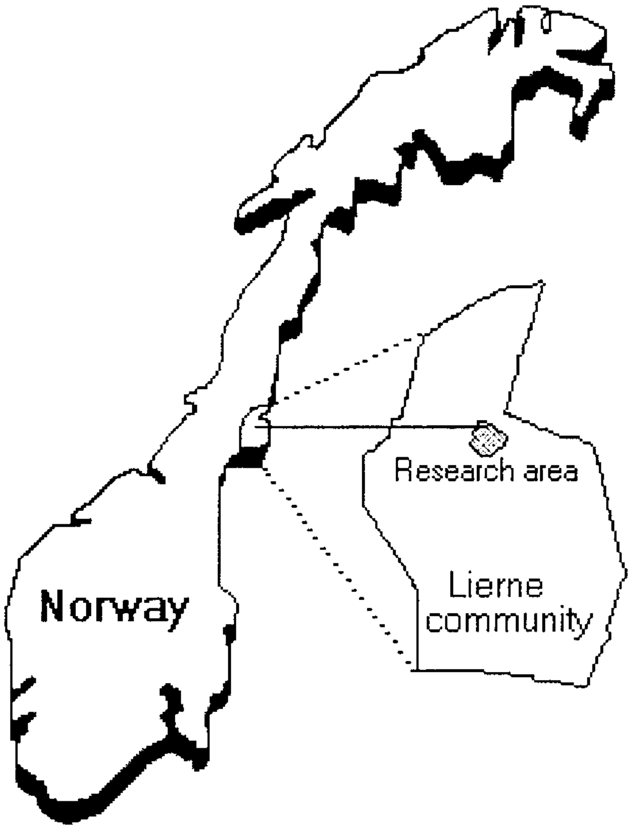

Fig. 1. Map of the research area "Holandsfjellet", located in the municipality of Lierne in Nord-Trøndelag county. A total of 624 sheep were grazing in the 3,500 ha combined mountain and forest range.

Table 1. Mean distances (m.; mean, SD, range) between dog and sheep and between dog and observer.

	Method A			Method B			Method C		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
	(m)			(m)			(m)		
Distance dog-sheep[1]	261	151.1	5–500	366	56.7	100–500	202	129.1	30–500
Distance dog-man	102	151.6	0-500	34	9.5	0-1000	15	34.3	0–500

[1]In 48% of the observations the data are missing because sheep were out of sight.

cedures (SAS 1987) were used: Mann-Whitney U-test and Student's t-test for testing the difference between 2 non-parametric and 2 parametric variables, respectively. Differences discussed are statistically significant of the 5% level unless otherwise stated.

Results

Behavioural Comparisons between Methods A, B and C

Using loose dogs without the command of a dog handler (Method A) was too uncontrolled under Norwegian conditions. The dogs ran to the nearby settlements, and they did not cover the area around the widely dispersed sheep sufficiently. They also chased wildlife (see below), and 9 domestic rabbits at a farm were killed. In addition, some dogs chased sheep. The episodes of chasing sheep became more aggravated, causing lambs to be separated from their mothers and possibly resulting in the death of 5 lambs. Because of the problems, it was not possible to collect sufficient amounts of data on Method A-dogs for statistical purposes.

Compared to the patrol dogs (dogs No. 2 and 3, Method B), pasture dogs (dogs No. 6 and 7, Method C) were >3 times as inactive (21% versus 76%, Fig. 2), and they were engaged in guarding activities half as often (19% versus 41%), but they barked 15 times more frequently. In addition to being observed from a fixed observing site, the pasture dogs were also observed for 4 hours (8 observation periods) when patrolling the enclosed area together with people. On these occasions the behavioral frequency distribution with respect to guarding, inactivity and other activities was 40%, 26%, and 35%, respectively. This is different from the activity pattern found when not guided (Mann-Whitney U-test), but nearly identical to the behavior shown by the patrol dogs (Fig. 2).

Within each working regime (B and C), differences in behavior between dogs were observed. Dog No. 3 was more inactive than dog No. 2 (Fig. 2), and dog No. 6 was more engaged in guarding activities compared to dog No. 7, particularly regarding barking, which he did >2 X as often.

Guarding Methods

The distance between dog and sheep was greater than the distance between dog and observer (t-test, Table 1). The dogs were 100 m or closer to the observer in 67% of the observations, but this close to the sheep only 4% of the times. These measures indicate that the dogs were more strongly socially bonded to people than to sheep. On some occasions exclusive to the observation periods the dogs ranged farther from the dog handler than Table 1 indicates. Maximum ranging distances were; method A: 10 km, method B: 2 km, and method C: 1 km (limited by the fence). The dogs wandered away less from the dog handler after rearranging the field trial (methods B and C versus method A), as intended.

During observation periods, dogs were observed confronting 31 woodland birds, 19 Lapland marmots (*Marmota* spp.), 4 moose (*Alces alces*) and a roe deer (*Capreolus capreolus*). In 85% of the cases the wildlife was chased/followed. About 50% of the marmots were attacked and killed.

Behavioral observations indicated there were at least 3 confrontations between the dogs and bears during the field study. The possible confrontations correspond well in time with findings of bear tracks and fresh sheep carcasses in the area.

Depredation and Economic Effect of Using Dogs

Little bear damage was recorded within the study area compared to the neighbouring areas until 24 August. Outside the study area depredation on sheep started 14 days earlier. However, some

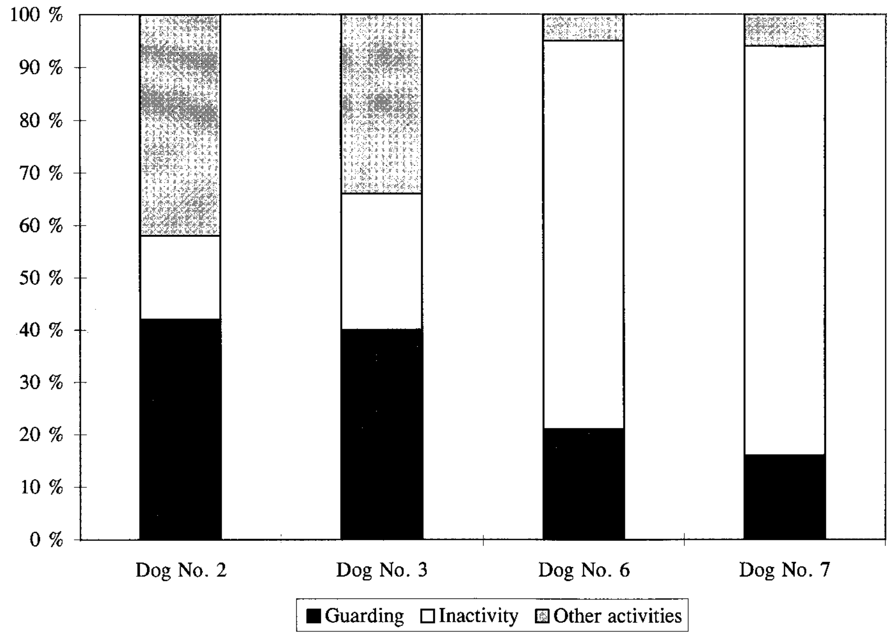

Fig. 2. Frequency distribution of the behavioral categories: guarding; inactivity; and other activities for dogs No. 2, 3 (patrol dogs), 6 and 7 (pasture dogs).

animals in the research herds (30–50%) periodically grazed outside the defined study area, and the majority of depredation in Herd I occurred outside the study area, where dogs were not used regularly (Table 2).

The pasture dogs expressed high frequencies of guarding activities (barking, patrolling), specifically on nights when sheep outside the fence were victims of depredation. Carcasses were not found inside the electric fence, whereas a ewe was killed and a lamb was injured only 200 m outside the fence.

The total loss on summer range (predators, disease and accidents) throughout the whole grazing season (7 June 7–15 October 1995) was 12.3% in Herd I and 10.8% in Herd II. Regarding the 2 research herds, the mean loss was reduced by 7% in 1995 compared to the 1994 grazing season, whereas the mean loss in the neighbouring herds (N=7) was reduced by 3.7 %. Compared to the mean loss on summer range during the last 3 years, the loss was 1.0 % lower in the research herds this year, while it was 0.6% higher in the neighbouring herds.

If a guarding dog in Norway is capable of working until the age of 7 (few accidental losses in Norway), it will have 6 effective guarding seasons. During these 7 years a Pyrenees will cost the owner about NOK 46,000 (U.S. $7,100) based on the mean costs for the puppy, food, veterinarian, dog yard, etc. (N=5). According to the 1995 compensation rates for sheep killed by large predators: NOK 1,760 ($270), lambs: NOK 920 ($140), a dog has to "save" at least 9 lambs or 5 ewes each working season before it will be an economical asset. Time spent for training and taking care of the dogs and special field costs as telemetric equipment, transportation, compensation for damages, etc. are not included in the cost calculations.

Table 2. Number of sheep and percent of total herd documented killed by bears in the two research herds during the research period 7 June –3 September 1995.

	Herd I				Herd II			
	Ewes		Lambs		Ewes		Lambs	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Bear kills within the research area	5	(3.4)	2	(0.9)	5	(5.4)	5	(3.2)
Total bear kills in the herd	17	(11.5)	2	(0.9)	5	(5.4)	5	(3.2)

Discussion

Method A–Loose Dogs

The use of loose dogs without the command of a dog handler was too unrestricted with respect to the strict Norwegian regulations for dog-keeping. Conflicts with neighbours are often caused by dogs when the herding area is close to settlements. The wandering problems were most likely a result of the imprinting procedure. If the dogs were more strongly bonded to sheep, they would be more attentive to them rather than ranging away (Coppinger et al. 1983, Lorenz and Coppinger 1986, Green and Woodruff 1990, Sims and Dawydiak 1990). The use of guarding dogs in the U.S. is a helpful management technique even on huge forest and mountain ranges, when the dogs are properly imprinted to sheep and the sheep flock close together (Hansen et al. 1996). Widely dispersing sheep complicate an adaptation of this technique to Norwegian conditions.

The sheep-chasing problems could have been avoided if the sheep had accepted the dogs as part of the flock. More attention should be focused on the significance of a mutual socialization between sheep and dogs. The socialization of sheep to dogs might take from a few days to years, depending on sheep breed, sheep management practices, and whether or not the dog shows the right submissive behavior (Aunsmo; Jacobson; Headly; Lorenz, pers. comm.).

Method B–Patrol Dogs

Patrol dogs showed a higher activity level than did the pasture dogs, because the observer in field moved around and contributed to dog activity. They barked far less than the dogs inside the pasture, and this way of using the dogs probably produced weaker preventive effects than Method C. Bear did kill sheep, despite that humans and dogs had vacated the site only a few hours previously, and their scent was obviously still present. It seemed as though the dogs had to encounter the bear directly and more than once before the bear would avoid the area. This is in accordance with other reports on bear-dog confrontations (Green and Woodruff 1989, Wikan 1996). In an arranged confrontation, autumn 1995, dogs No. 2, 6, and 7 were released on a radio-tracked bear (Hansen and Bakken 1999). The dogs encountered the bear and chased him for 25 minutes, but the bear returned within 1 hour.

The use of guarding dogs under the command of a dog handler is resource-demanding. To make the patrolling more effective, one could give priority to areas where fresh carcasses are found. However, guarding dog experts in the U.S. do not believe in using handlers (Jacobson; Hansmire; Lorenz; Woodruff; Coppinger, pers.comm.), because the full capacity of the dog's livestock-guarding behavior is actually not utilized.

Method C–Pasture Dogs

The pasture dogs guarded a rather small territory around their feeding site. They barked frequently, but ran off to the other side of the pasture (1 km) only a few times. There were no losses due to predation within the pasture. However, the dogs' guarding effect is unclear, since the electric fence might have helped prohibit bear damage, although the electricity was turned off at night.

A close connection to people functioned well for the patrol dogs, but not for pasture dogs. If they were left alone (loose), they jumped the electric fence and sought out people. The use of guarding dogs in pastures without handlers is an effective method only if the dogs are properly imprinted to sheep and stay with them (Coppinger et al. 1983, Lorenz and Coppinger 1986, Green and Woodruff 1990, Sims and Dawydiak 1990).

Effect of Using Guarding Dogs

Most of the depredation in Herd I occurred outside the research area where dogs were not used regularly, and the total number of sheep lost on summer range was relatively greater in neighbouring herds than in research herds. However, the single effect of using guarding dogs in this research remains unclear. In contrast to earlier years, the managers of the 2 most heavily depredated herds had now stopped sheep farming, and there had never before been traffic by dogs and people in the area at night.

From the end of August until the end of the research period, it seemed impossible to guard the herding area sufficiently. This was probably due to more bears entering the area, too few dogs to cover the whole range, and darker nights (the research area does not have the midnight sun) which made it impossible to patrol at night.

To fully realize guarding dog capabilities (Lorenz and Coppinger 1986, Coppinger et al. 1988, Green and Woodruff 1990, Andelt 1992), conditions must be adapted to the dog rather than attempting to change the dog. Before guarding dogs can be effective in Norway, we need either a sheep breed that flocks well or we need to reintroduce shepherding, or we need enclosed grazing areas. Under the U.S. conditions, one shepherd can manage 1,000 sheep, and only 2 to 5 dogs are needed to guard the flock (Hansen et al. 1996). High compensation rates for livestock losses and high costs for dog-keeping in Norway require the efficiency of guarding dogs in Norway to be even greater than that observed in the U.S. (Green et al. 1984, Andelt 1992) before this method can be economically feasible.

Socialization Program and Guarding Techniques

The socialization program followed (introducing the dogs to sheep at 12–16 weeks of age, with frequent association with people) is not the one recommended by guarding dog researchers (Coppinger et al. 1983, Lorenz and Coppinger 1986, Viner, pers. comm.). The error is obvious; too late and too weak social imprinting to sheep resulted in dogs bonded socially closer to people than to sheep. Consequently, these dogs were not attentive to sheep, and they did not guard sheep without the presence of people.

There is a conflict between the Norwegian Kennel Club and behaviourists about how to rear the pup to get the best guarding behavior adapted to the strict and specific Norwegian conditions. We argue that the degree of social imprinting of the puppy on sheep versus people is dependent on the future guarding method planned. Is the dog going to work under the command of a dog handler or independently among sheep? Is it going to work within its own flock of sheep or in a common herding area? The less command by people, the stronger the social bonding to sheep that is required.

Conclusions and Management Implications

It is difficult to use guarding dogs the traditional way in Norway because of the open mountain/forest range and widely dispersing sheep. Based on our results, we suggest 3 alternative management procedures:

1. Guarding dogs working among sheep inside a fenced area. This will be an effective way of guarding sheep only if the dogs are socially bonded to sheep and the sheep accept the dogs as part of their flock.

2. Guarding dogs patrolling the herding area under the command of a dog handler. The dogs must be socialized to people as well as to sheep. Preferably, the dogs are used only during the night.

3. Guarding dogs on unfenced forest/mountain range, using a herder and/or a sheep breed with closer flock characteristics, dogs closely bonded to sheep, and sheep who accept the dogs. In the most severely affected areas we recommend this method, even though it requires changing the Norway sheep grazing management used on open range.

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First limiting nutrient for summer calving cows grazing autumn-winter range

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Abstract

Two trials were conducted in 1994, 1995, and 1996 to determine the first limiting nutrient for summer calving cows grazing Sandhills range. In Trial 1, 48 lactating summer calving cows grazing native range during the breeding season were assigned to 1 of 4 supplement treatments: 1) control-no supplement, 2) energy, 3) degradable intake protein (DIP), and 4) DIP + undegraded intake protein (UIP). Cows were group-fed supplements in 8 pastures (2 pastures/treatment). The trial began 4 September and ended 4 November each year. Diet samples from esophageally fistulated cows averaged 7.5% crude protein and 54.5% in vitro organic matter digestibility. Supplemented cows lost less body condition compared to control cows (P = 0.04). Cow and calf weight gains were increased by supplemental DIP or DIP + UIP combination compared to energy supplement (P = 0.09 and 0.08, respectively). Forage intake and digestibility were not different among treatments (P>0.20). Milk production was lower for non-supplemented than supplemented cows (P = 0.10). Trial 2 began 5 November and ended 10 January in 1994-1995, 1995-1996, and 1996–1997. Treatments and pastures were the same as described in Trial 1, however, only 40 cows were used. In Trial 2, diet samples from esophageally fistulated cows averaged 6.2% crude protein and 52.3% in vitro organic matter digestibility. No differences (P>0.10) in body condition score were detected. Total organic matter intake was lower for control compared to supplemented treatments (13.5 vs.15.5 kg day^{-1}; P < 0.10). We concluded that DIP was the first limiting nutrient for summer calving cows during the breeding season and during autumn-winter lactation after the breeding season.

Key Words: Supplementation, forage intake, forage digestibility, rumen degradable protein, undegraded intake protein

Resumen

Durante 1994, 1995, y 1996 se condujeron dos ensayos para determinar el el primer nutriente limitante para vacas amamantando durante el verano y apacentando pastizales “Sandhills”. En el ensayo 1, 48 vacas lactantes amamantando en verano y apacentando pastizal nativo durante la época de empadre fueron asignadas a 1 de 4 tratamientos de suplementación: 1) sin suplemento (control), 2) energía, 3) consumo de proteína degradable (DIP) y 4) DIP + consumo de proteína no degradada (UIP) Las vacas fueron agrupadas por suplemento en 8 potreros (2 potreros/tratamiento). El estudio inició el 4 de Septiembre y terminó el 4 de Noviembre de cada año. Las muestras de la dieta obtenidas de vacas con fístula de esófago promediaron 7.5% de proteína cruda y 54.5% de digestibilidad in vitro de la materia orgánica. Las vacas suplementadas perdieron menos condición corporal comparadas con las vacas del tratamiento control (P = 0.04). Las ganacias de peso de la vaca y el becerro incrementaron por la suplementacion DIP o la combinación DIP + UIP en comparación con el suplemeto de energía (P = 0.09 y 0.08 respectivamente). El consumo de forraj y la digestibilidad no difirieron entre tratamientos (P>0.20). La producción de leche fue menor para las vacas no suplementadas que para las suplemetadas (P = 0.10). El ensayo 2 inició en Noviembre 5 y teminó en Enero 10 de 1994–1995, 1995–1996, y 1996–1997. Los tratamientos y potreros fueron los mismos descritos en el ensayo 1, sin embargo, solo 40 vacas fueron utilizadas. En el ensayo 2, las muestras de la dieta colectadas vía fístula esofágica promediaron 6.2% de proteína cruda y 52.3% de digestibilidad in vitro de la materia orgánica. No se detectaron diferencias (P>0.10) en la calificación de la condición corporal. El consumo total de materia orgánica fue menor para el grupo control comparado con los tratamientos suplementados (13.5 vs 15.5 kg dia-1; P<0.01). Concluimos que DIP fue el primer nutriente limitante para vacas amamantando en verano durante la época de empadre y durante la lactación de otoño-invierno después de la época de empadre.

Nutrient requirements of beef cattle have been well defined (NRC 1996). However, nutrient intake of grazing cattle is not well defined due to problems associated with measurement of forage intake and digestibility of grazing cattle. Data related to supplementation of spring (Blasi et al. 1991, Sowell et al. 1992, Marston and Lusby 1995, Marston et al. 1995) and autumn calving cows (Rakestraw et al. 1986, Gonzalez et al. 1988, Hibberd et al. 1988, Ovenell et al. 1989) are plentiful in

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the literature. However, limited information is available regarding whether energy or protein is first limiting for lactating summer calving cows grazing native range during the autumn-winter months.

Warm-season grasses on Nebraska Sandhills range decline in quality in late summer, a time corresponding to the breeding season for the summer calving cow (Lardy 1997). We hypothesized that summer calving cows would respond to undegraded intake protein (UIP; as defined by NRC 1996), in addition to degraded intake protein (DIP; as defined by NRC 1996) due to the demands of lactation on metabolizable protein requirements. Our objectives were to determine whether energy, DIP, or DIP + UIP was the first limiting nutrient for lactating summer calving cows grazing native range during the breeding season and late lactation.

Materials and Methods

Trial 1

The study was conducted on native range at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (elevation 1,073 m, 42° 05' north latitude, 101° 26' west longitude) near Whitman, Neb. Forty-eight lactating MARC II crossbred (1/4 Hereford, 1/4 Angus, 1/4 Simmental, and 1/4 Gelbvieh) multiparous summer calving (avg calving date = 1 July) beef cows and their calves were assigned to 4 replicated supplement treatments from 4 September to 4 November in 1994 (body weight = 578.4 kg ± 53), 1995 (body weight = 590 kg ± 55), and 1996 (body weight = 601 kg ± 58). Treatments were assigned randomly to pastures (i.e., replicates) each year. Cows were stratified by calving date and calf sex and assigned to pastures at the initiation of the trial. Treatments were: 1) control, no supplement; 2) control and supplemental energy, fed at isocaloric levels to the protein supplements; 3) Degraded intake protein (DIP) supplement; and 4) DIP + undegraded intake protein (UIP) combination. Composition of supplements is given in Table 1. Supplements were not isonitrogenous, but were formulated to meet calculated requirements for DIP and metabolizable protein (NRC 1996). In 1994 and 1995 cows were group-fed their supplements daily in 35.6 hectare pastures. In 1996, cows were fed supplements 4 times week^{-1}.

Table 1. Composition (g day^{-1}) of protein and energy supplements fed in Trial 1.

Item	Treatment: Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)
	(g day^{-1})			
Soyhulls	—	425	153	—
Tallow-	—	47	17	—
Corn steep liquor	—	—	284	—
Sulfite liquor treated soybean meal	—	—	—	470
Feather meal	—	—	—	118

The estimated DIP requirement was 663 g, of which 555 g was supplied by the forage. These estimates were based on the assumptions that the average cow weighed 545 kg and would consume a 53% total digestible nutrients (TDN) forage at 2.3% of body weight) Hollingsworth-Jenkins 1994). Net synthesis of bacterial crude protein was assumed to be 10% of the TDN intake (Burroughs et al. 1974, Villalobos 1993). The degraded intake protein (DIP) content of the forage was estimated to be 4.44% of organic matter (OM; Hollingsworth-Jenkins et al. 1996). Corn steep liquor, a byproduct of the wet corn milling industry, is 38% crude protein, of which 100% is DIP (Karges 1990). The metabolizable protein requirement was estimated to be 720 g, which was based on an average body weight of 545 kg and a peak milk production of 8.2 kg day^{-1}. The forage was assumed to supply 125 g of metabolizable protein and bacteria would supply 424 g (12.5 kg dry matter intake X 53% TDN X 10% efficiency X 80% true protein X 80% digestibility; NRC 1996). The sulfite liquor treated soybean (Glycine max L. Merr) meal:feather meal supplement was estimated to be 52% crude protein, of which 70% was undegraded intake protein (UIP) (Britton et al. 1978). Therefore, the sulfite liquor treated soybean meal:feather meal supplement provided both DIP and UIP. The energy supplement, DIP supplement, and the DIP and UIP supplement were formulated to be isocaloric. The energy supplement was not intended to meet the energy requirements of the cows but provided an isocaloric control to determine if energy and not DIP or the DIP + UIP were the first limiting nutrients.

The range was sands and choppy sands sites. The soil was Valentine fine sands (mixed, mesic, ustpamments). The dominant grass species on the native range pastures were: little bluestem [*Schizachrium scoparium* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem (*Andropogon gerardii* var. *paucipilus* Hack.), switchgrass (*Panicum virgatum* L.), sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], indiangrass [*Sorghastrum nutrans* (L.) Nash], and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]. Common forbs and shrubs included western ragweed (*Ambrosia psilostachya* DC.) and leadplant [Amorpha canescens (Nutt.) Pursh].

Cows and calves were weighed and cows scored for body condition at the beginning and end of the trial. Body condition scores were based on a palpated determination of fleshing over the ribs and thoracic vertebrae. Body condition was scored from 1 (thinnest) to 9 (fattest) according to the system described by Richards et al. (1986).

Fecal output for estimation of forage intake was determined on 24 cows (6 cows/treatment) during September and again in October of 1994 and 1995. Sample collection dates were 15 September through 19 September, 1994; 29 October through 2 November, 1994; 18 September through 22 September, 1995; and 24 October through 27 October, 1995. Three cows were selected randomly from each pasture and brought to a common pasture for intake determinations. The common pasture was located adjacent to the treatment pastures and was also a choppy sands site with similar forage characteristics as treatment pastures. The use of a common pasture facilitated individual feeding and fecal collection procedures necessary to measure fecal output. Cows remained in the common pasture for 10 days during each collection period. Cows were individually fed supplements for 5 days before intake determinations and during the fecal collection period. During the October 1995 collection period, a blizzard prevented collection of samples over a 5-day period; consequently, samples were only collected over 4 days. Each cow on the intake trial was orally dosed with an intraruminal continuous chromium (Cr)-releasing device[1] 5 days before the 5-day fecal collection period. Three hundred to 500 g of feces were obtained from the rectum of each cow daily at about 0800 hours. Forage intake was estimated by dividing fecal output by the indigestibility of the forage diet after accounting for the supplement (Kartchner 1980).

Total fecal collections were taken from 6 steers in September 1994 and 5 steers in September and October 1995. Total fecal collections were not made in October 1994. The correction factor from the September 1994 collection period was assumed to represent the data collected in October 1994 because boluses were manufactured in the same lot and forage was similar. Steers used for total fecal collection received no supplement (Hollingsworth et al. 1995). Steers were dosed with the same intraruminal continuous Cr releasing device as the cows on the trial and fitted with fecal collection bags for total fecal collection to obtain a correction factor for fecal output (Adams et al. 1991a, Hollingsworth et al. 1995). Feces collected in fecal collection bags were weighed, mixed, subsampled (300 to 500 g), and bags emptied. In September 1994 and September 1995, bags were emptied twice daily at 0800 and 1700 hours during the 5-day fecal collection period. In October 1995, feces were lower in moisture and fecal bags were emptied once daily at 0800 hours.

Forage diet samples were collected in September and October of 1994 and 1995 using 6 to 8 esophageally fistulated cows. Diet samples were collected in the pasture designated for the forage intake determination. Cows were held off feed overnight and allowed to graze for 20 to 40 minutes for sample collections. Cows had been fistulated for 1 to 4 years previously as described by Adams et al. (1991b) with modifications for adult cattle. The surgical preparation and post-surgical care procedures were reviewed and approved by the University of Nebraska Institutional Animal Care and Use Committee. Diet extrusia samples were collected in screen bottom bags and immediately frozen.

Milk production was measured using the weigh-suckle-weigh technique on 23 September 1995, 28 October 1995, 19 October 1996, and 5 November 1996. Three cows from each pasture (6/treatment) were randomly selected for measurement of milk production at each time. Pregnancy was determined by rectal palpation approximately 70 days following the conclusion of the breeding season.

All fecal and extrusa samples were stored frozen until chemical analyses were performed. Extrusa and fecal samples were freeze dried. Fecal samples were ground to pass through a 1-mm screen in a Wiley Mill. Extrusa samples were ground to pass through a 2-mm screen in a Wiley Mill for analysis of diet protein degradability. Extrusa samples were ground to pass through a 1-mm screen in a Wiley Mill for analysis of dry matter, organic matter, crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), and in vitro organic matter digestibility (IVOMD). Dry matter, organic matter, and crude protein were determined by standard methods (AOAC 1990). Neutral detergent fiber was determined according to Van Soest et al. (1991), and ADF by the method of Van Soest (1963). In vitro organic matter digestibility of extrusa samples was determined by the modified procedures of Tilley and Terry (1963) with the addition of 1 g of urea to the inoculum-buffer mixture (Weiss 1994). Inoculum from 2 steers, 1 fed a grass hay diet and 1 fed a corn cob diet supplemented with soybean meal, was mixed in a 50:50 ratio with prewarmed (39°C) McDougall's solution. Samples were incubated for 48 hours with inoculum:buffer mixture followed by 24-hour pepsin digestion. Fecal samples were analyzed for chromium concentration by atomic absorption spectrophotometry using an air plus acetylene flame (Williams et al. 1962).

Undegraded intake protein (UIP) of extrusa samples was determined by the method of Mass et al. (1996). Briefly, 5 g samples were incubated in dacron bags[2]. Samples were incubated for 2, 12, and 96 hours. Three separate incubation runs were performed over 3 days. Bags were washed according to Wilkerson et al. (1995) and subjected to analysis of neutral detergent fiber nitrogen. Amounts of neutral detergent fiber nitrogen remaining after incubation were log transformed and a rate of degradation calculated. The UIP was calculated using the following formula: $UIP = B \times (k_p/(k_d+k_p)) + C$; where B is the pool size or potential UIP calculated from the intercept of the log transformation of degradation, k_p is the rate of passage, k_d is the rate of degradation of neutral detergent fiber nitrogen, and C is the undegradable fraction (Broderick 1994). Passage rates were determined at the Gudmundsen Sandhills Laboratory by Lamb (1996). The UIP content of the sulfite-liquor treated soybean meal-feather meal supplement fed in this study was determined using the ammonia release procedure of Britton et al. (1978).

Data were analyzed using the MIXED procedures of SAS (1990) appropriate for a repeated measures design. For body weight, body condition score, and pregnancy data, pasture within treatment was considered random. Treatment effects were tested using pasture within treatment as the error term. Year and year X treatment interaction were tested using the residual error. For intake data, pasture within treatment and year X pasture within treatment were considered random. Treatment effects were tested using pasture within treatment as the error term. Year and the year X treatment interaction were tested using year X pasture within treatment. Period, period X treatment, period X year, and period X treatment X year were tested using the residual error term. For milk production data, year X period X treatment was considered random. Treatment, period, year, and the 2-way interactions were tested using year X period X treatment as the error term. For all data, pre-

[1]Captec Chrome manufactured by Captec Pty. Ltd., Australia, distributed internationally by Nufarm Limited, Manu Street, P.O. Box 22-407, Otahunu, Auckland 6, New Zealand.

[2]Ankom, Inc., Fairport, N.Y.

planned contrasts were used to compare: 1) the control vs all supplemented treatments, 2) the energy control vs degraded intake protein (DIP) supplement + DIP + UIP combination, and 3) DIP vs DIP + UIP combination. Pregnancy data were transformed using the arc sine of the square root before analysis (Snedecor and Cochran 1989).

Trial 2

The study was conducted on native range at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory in the same pastures as described for Trial 1. Forty lactating MARC II crossbred summer calving beef cows were assigned to 4 supplement treatments from 5 November to 10 January in 1994–95 (body weight = 578 kg ± 55), 1995–96 (body weight = 575 kg ± 47), and 1996–97 (body weight = 608 kg ± 58). Supplement composition is given in Table 2. Experimental protocols followed in Trial 2 were the same as used in Trial 1.

Assumptions used to calculate supplemental needs in Trial 2 were the same as in Trial 1 with the following exceptions. Diet crude protein was assumed to be 5%, with 2.95% of the organic matter as degraded intake protein (DIP), and 2.05% undegraded intake protein (UIP). Diet in vitro organic matter digestibility was assumed to be 57%. The DIP requirements were calculated using 8% microbial efficiency. For Trial 2 in 1994 and 1995, the amount of DIP in the DIP + UIP supplement was inadequate in DIP. In 1996, the amount of DIP in the DIP + UIP supplement was increased (Table 2).

Fecal output for determination of forage intake was measured on 24 cows (6 cows/treatment) during December of 1994 and 1995. Sample collection dates were 7 December to 12 December 1994 and 12 December to 16 December 1995. Total fecal collections were made using 5 steers in 1994 and 6 steers in 1995 to obtain a correction factor for chromium release rate from the bolus as described for Trial 1. Forage intake was calculated as described for Trial 1.

Milk production was measured using the weigh-suckle-weigh technique on 16 December 1995 and 13 December 1996. Storage, preparation, and analysis of diet and fecal samples followed the procedures described in Trial 1.

Table 2. Composition (g day^{-1}) of protein and energy supplements fed in Trial 2.

	Treatment			
Item	Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)
Years 1 and 2	(g day^{-1})			
Soyhulls	—	425	—	288
Tallow	—	47	—	32
Corn steep liquor	—	—	508	—
Sulfite liquor treated soybean meal	—	—	—	175
Feather Meal	—	—	—	44
Year 3				
Soyhulls	—	499	75	—
Tallow	—	55	8	—
Corn steep liquor	—	—	508	426
Sulfite liquor treated soybean meal	—	—	—	159
Feather Meal	—	—	—	40

Data from Trial 2 were analyzed using the assumptions, procedures and preplanned contrasts described for Trial 1. For Trial 1 and Trial 2, significant differences are noted at P<0.10.

Results and Discussion

Trial 1

Table 3 shows precipitation and temperatures for the months during which the trial was conducted and the long term averages. Average ambient temperatures during the trials were generally cooler than average, and yearly precipitation was 6% higher than average in 1994 and 57% higher than average in 1995.

Diet samples averaged 7.5% crude protein, 1.4% undegraded intake protein (UIP), and 55% in vitro organic matter disappearance during the breeding season (Table 4). The degraded intake protein (DIP) and digestibility values of the diets selected were similar to the estimates used to formulate the supplements. However, the crude protein level was 1.8 percentage units higher than expected.

Year effects were detected for initial cow body condition, weight change, calf weight gain, body condition score change, and final body condition score (P = 0.004, P = 0.12, P = 0.003, P = 0.0002, and P = 0.004, respectively). However, year by treatment interactions were not detected for these variables (P = 0.88, P = 1.00, P = 0.17, P = 0.65, and P = 0.57, respectively).

Cow weight loss was greater (P = 0.08) for control cows than the mean of cows receiving supplements (Table 5). Cows supplemented with DIP and DIP + UIP lost less weight compared to cows receiving the energy supplement (P = 0.09). No differences were detected when DIP and DIP + UIP supplements were compared (P = 0.23). This is inconsistent with the findings of Dhuyvetter et al. (1992) who reported decreased weight loss when lactating

Table 3. Monthly and yearly precipitation and temperature profiles for 1994 and 1995 at the Gudmundsen Sandhills Laboratory, Whitman, Neb.

	Date					
	Sept.	Oct.	Nov.	Dec.	Annual	Average (1982–1994)[1]
1994 Precipitation (cm)	3.00	3.58	1.88	1.93	59.33	56.03
1994 Avg. daily temperature (°C)	17.2	9.9	1.7	-0.3	8.9	9.8
1995 Precipitation (cm)	14.63	11.66	1.02	0.51	88.29	56.03
1995 Avg. daily temperature (°C)	15.6	8.3	2.1	–2.0	8.4	9.8

[1]Collection of weather data began in 1982.

Table 4. Percentage crude protein (CP), undegraded intake protein (UIP), neutral detergent fiber (NDF), acid detergent fiber (ADF) concentrations, and in vitro organic matter digestibility (IVOMD) of diets collected from esophageally-fistulated cows grazing native range during Trial 1 (OM Basis).

Date	CP	UIP	NDF	ADF	IVOMD
			%		
17 Sep 1994	7.79	0.63	80.9	50.2	59.5
3 Nov 1994	5.89	0.93	84.4	56.1	48.3
9 Sep 1995	9.20	2.33	68.1	46.1	53.8
26 Oct 1995	7.09	1.54	80.1	51.6	56.8

spring calving cows were supplemented with supplements containing 50% of the supplemental protein as UIP compared with supplements containing 25% of the supplemental protein as UIP. Hibberd et al. (1988) reported decreased weight loss in lactating autumn calving cows when fed supplements containing increased levels of UIP. Triplett et al. (1995) reported no difference in weight or body condition score changes of mature and primiparous cows fed low, medium, or high UIP supplements while grazing rye (*Secale cereale* L.)-ryegrass (*Lolium perenne* L.) overseeded into Coastal bermudagrass [*Cynodon dactylon* (L.) Pers.] pastures. Blasi et al. (1991) reported no differences in weight gain for lactating spring calving cows grazing big bluestem pastures and supplemented with increasing levels of UIP.

Body condition score loss was greater for cows on the control treatment (P = 0.04, Table 5) than cows that received a supplement. Short et al. (1996) reported spring calving cows grazing native range during the autumn and supplemented with a cottonseed meal (Gossypium spp.) based supplement gained more weight and body condition than cows receiving no supplement. Marston et al. (1995) reported similar body weight loss when either a protein (soybean meal based) or an energy (soyhull based) supplement were fed to provide similar amounts of crude protein for lactating spring calving cows grazing native range. In the work of Marston et al. (1995), the energy supplement provided approximately 2 times the metabolizable energy of the protein supplement. The sulfite liquor treated soybean meal-feather meal combination used in the DIP + UIP treatment would supply more UIP than cottonseed meal or soybean meal based supplements used by Short et al. (1996) and Marston et al. (1995), respectively. No difference in body condition score change was detected among the supplements (P>0.45, Table 5).

Control cows tended (P = 0.16) to have lower conception rates (87.5% vs 95.8%) than the mean of the supplemented cows. Triplett et al. (1995) found higher first service conception rates for cows fed medium and high UIP supplements than for cows fed a low UIP supplement. Pregnancy rate was not the primary criteria by which we intended to evaluate the effects of supplementation. However, this trend does merit further investigation with larger numbers of cows. Dhuyvetter et al. (1992) found no differences in pregnancy rates when cows were supplemented with either 25 or 50% UIP.

Calves nursing control cows gained less weight than calves which nursed cows receiving supplements (P = 0.03). Calves nursing cows receiving supplemental protein gained more weight than calves nursing cows receiving the energy supplement (P = 0.08). Cows consumed supplements rapidly and calves

Table 5. Least squares means for initial body condition score, final body condition score, body condition score change, initial cow weight, final cow weight, cow weight change, initial calf weight, final calf weight, calf weight gain, and pregnancy rate during Trial 1.

	Treatment					
Item	Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)	SE[1]	Contrast[2]
Initial BCS	5.76	5.57	5.63	5.57	0.08	NS[3]
Final BCS	5.13	5.17	5.27	5.28	0.09	NS
BCS change	–.63	–.40	-.36	–.29	0.08	1
			(kg)			
Cow initial weight	590.5	578.2	592.3	597.6	5.18	2
Cow final weight	571.4	563.1	585.1	599.7	6.84	2
Cow weight change	–19.1	–15.1	–7.1	2.0	4.60	1, 2
Calf initial weight	109.1	104.4	107.6	105.5	2.63	NS
Calf final weight	162.0	161.0	168.9	167.7	3.32	NS
Calf weight gain	52.9	56.6	61.3	62.2	1.85	1, 2
24-hr milk production	5.69	6.06	7.59	6.98	0.52	1
			Number cows bred/number exposed			
Pregnancy[4]	33/36	35/36	35/36	35/36	0.07	NS

[1]SE, Standard error of the mean.
[2]Contrasts: 1, control vs. supplemented treatments; 2, energy vs. degraded intake protein + degraded intake protein undegraded intake protein combination; 3, degraded intake protein vs. degraded intake protein undegraded intake protein combination.
[3]NS, Not significant (P>0.10)
[4]Pregnancy rate analyzed as the arc sine transformation of the proportion of number bred divided by the number exposed.

Table 6. Least squares means for forage intake and total intake (e.g. forage plus supplement) for summer calving cows grazing autumn range in Trial 1.

Item	Treatment					
	Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)	SE[1]	Contrast[2]
Forage intake (kg organic matter day^{-1})	16.7	16.6	17.8	15.8	0.79	NS[3]
Total intake (kg organic matter day^{-1})	16.7	17.1	18.3	16.4	0.77	NS
Forage intake (kg/100 kg body weight^{-1} day^{-1})	2.95	2.87	3.15	2.72	0.144	NS
Total intake (kg/100 kg body weight^{-1} day^{-1})	2.95	2.95	3.23	2.82	0.146	NS

[1]SE, Standard error of the mean.
[2]Contrasts: 1, control vs. supplemented treatments; 2, energy vs. degraded intake protein + degraded intake protein undegraded intake protein combination; 3, degraded intake protein vs. degraded intake protein undegraded intake protein combination.

were not given access to supplements; consequently, increased calf weight gain was not influenced by calf consumption of supplements. Milk production (Table 5) was higher for supplemented cows than for control cows (P = 0.10). Milk represents an important source of nutrients for growing calves (Baker et al. 1976, Lamb et al. 1997, Lardy 1997). Milk production was not different when lactating spring calving cows were fed increasing levels of undegraded intake protein (UIP) while grazing big bluestem pastures (Blasi et al. 1991). Cows fed high UIP supplements produced more milk. Milk production also increased when cows were fed higher amounts of TDN (Hibberd et al. 1988). No differences in milk production or calf weight gain were found when cows were fed supplements containing low, medium, or high UIP levels (Triplett et al. 1995). Cows fed 100 g UIP/day produced more milk than cows fed 200 g UIP/day when grazing endophyte [*Neotyphodium coenophialum* Morgan-Jones and Gams (Glen, Bacon, and Hanlin)]-infected tall fescue (*Festuca arundinacea* Schreb.; Forcherio et al. 1995). In addition, calves nursing cows receiving 100 g UIP/day gained more weight compared to calves nursing cows receiving 200 g UIP protein/day (Forcherio et al. 1995). Milk production increased linearly in cows given low quality hay and supplemented with increasing levels of a protein supplement based on a blend of cottonseed meal, fish meal, and meat meal (Lee et al. 1985). In contrast, Hunter and Magner (1988) found that milk production was not affected by supplementation in the first 8 weeks of lactation and during late lactation milk production was decreased when heifers were supplemented with formaldehyde-treated casein.

No differences (P>0.45) were detected in forage intake or total intake (e.g., forage plus supplement) on a kg/100 kg body weight basis among treatments (Table 6). Marston and Lusby (1995) found lactating spring calving cows fed a soybean meal based protein supplement had higher hay dry matter intake than cows fed a soyhull based energy supplement. Marston and Lusby (1995) found hay digestibility was higher for the protein supplemented cows in year 2 but not in year 1. Forage intakes and forage digestibility were lower for cows supplemented with protein compared to cows receiving no supplement (Short et al. 1996).

Period by year interactions (P = 0.03) were detected for forage intake, total intake, forage intake as a percentage of body weight, total intake as a percentage of body weight, and digestibility (Table 7). Significant snowfall events occurred during the collection period in 1995, which possibly influenced grazing behavior of the cows (Adams et al. 1986), consequently affecting intake and digestibility. During the September 1995 collection period, snow only remained on the ground 2 days. During the October 1995 collection period, snow remained on the ground throughout the collection period. The September snowfall event and colder temperatures may have caused the reductions in forage intake observed when comparing September 1994 to September 1995 (Adams et al. 1986). The in vitro organic matter digestibility of the samples indicated lower digestibility in November 1994 compared to October 1995 (Table 4). An explanation for the low digestibility observed in November

Table 7. Least squares means forage intake and total intake (e.g. forage plus supplement) for summer calving cows grazing autumn range by period and year in Trial 1.

Item	September		October		Period X year interaction
	Year 1	Year 2	Year 1	Year 2	P value
Forage intake (kg organic matter day^{-1})	19.9	16.3	15.4	15.3	0.03
Total intake (kg organic matter day^{-1})	20.3	16.7	15.8	15.7	0.03
Forage intake (kg/100 kg body weight day^{-1})	3.45	2.82	2.72	2.69	0.038
Total intake (kg/100 kg body weight day^{-1})	3.52	2.88	2.79	2.75	0.039
	Climatic data during intake determinations				
Snowfall (cm)	—	20.3	—	40.6	—
Average high temp (°C)	26.3	10.9	17.6	10.6	—
Average low temp (°C)	5.8	0.9	-3.0	–3.2	

1994 compared to October 1995 is not readily apparent.

The fact that cows did not respond to undegraded intake protein (UIP) in addition to degraded intake protein (DIP) did not fit our hypothesis. Several things likely influenced this lack of response. Forage intake was higher than expected, which results in higher bacterial crude protein production in addition to more total forage protein escaping from the rumen. Metabolizable protein supply would be increased by 114 g due to the increased intake (3.27 kg additional intake X 10% efficiency X 80% digestibility X 80% true protein), metabolizable protein supply would also increase by 35 g (3.27 kg additional intake X 1.35% UIP X 80% digestibility) due to additional UIP from the forage. In addition, milk production was lower than expected which reduces the metabolizable protein requirement. This results in a metabolizable protein requirement of 796 g and a metabolizable protein supply of 698 g. Based on measured intakes, digestibility, protein degradability, and milk production, the magnitude of the difference between the metabolizable protein requirement and supply was smaller than expected, which may explain the lack of response to the additional UIP. In addition, the fact that milk production was higher for cows receiving supplements would tend to reduce the magnitude of a response in weight change or body condition score change, because nutrients would be partitioned toward milk production rather than energy reserves for the cow.

Table 8. Percentage crude protein (CP), undegraded intake protein (UIP), neutral detergent fiber (NDF), acid detergent fiber (ADF) concentrations, and in vitro organic matter digestibility (IVOMD) of diets collected from esophageally-fistulated cows grazing native range during Trial 2 (organic matter basis).

Date	CP	UIP	NDF	ADF	IVOMD
	- - - - - - - -	- - - - - - - -	(%)	- - - - - - - -	- - - - - - - -
12 Dec 1994	5.89	0.85	85.0	54.1	48.4
12 Dec 1995	6.54	1.44	78.0	49.1	56.2

Another variable that affects metabolizable protein supply is the efficiency of conversion of TDN to bacterial crude protein. With high quality forages, a 13% efficiency is used by NRC (1996). However, with low quality forages, lower efficiencies (7 to 10%) have been measured (Villalobos 1993, Hollingsworth-Jenkins et al. 1996, NRC 1996). Reductions in passage rate with low quality forages increase maintenance requirements because proportionally more energy is used for bacterial maintenance rather than growth. Hollingsworth-Jenkins et al. (1996) used non-lactating gestating beef cows and Villalobos (1993) used steers fed low quality prairie hay to determine these efficiencies. Hollingsworth-Jenkins et al. (1996) reported organic matter intakes of 2.1% of body weight, while the intakes reported here are considerably higher. Passage rate increases with increased intake (Adams and Kartchner 1984); microbial efficiency may also increase with increases in passage rate. The beef cattle nutrient requirements model (NRC 1996) was used to calculate the microbial efficiency at which degraded intake protein (DIP) supply was equal to DIP requirement. For these calculations, we assumed that the DIP and DIP + undegraded intake protein (UIP) supplements both met the DIP requirement. These calculations indicated that the microbial efficiency was 11% rather than 10% as we used in formulating supplements. The net effect of a greater efficiency would be to increase the amount of DIP required and increase the amount of metabolizable protein supplied (NRC 1996). This would also help to explain the lack of response to supplemental UIP.

Trial 2

Five cm of snow remained on the ground throughout the December 1994 collection period. No snowfall was recorded during the December 1995 collection period. Average high and low temperatures were –0.6°C and –12.8°C during the December 1994 collection period and 9.4°C and 5.9°C during the December 1995 collection periods.

Table 9. Least squares means for initial body condition score, final body condition score, body condition score change, initial cow weight, final cow weight, cow weight change, initial calf weight, final calf weight, and calf weight gain during Trial 2.

	Treatment					
Item	Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)	SE[1]	Contrast[2]
Initial BCS	5.10	5.13	5.29	5.34	0.10	NS
Final BCS	4.17	4.38	4.41	4.71	0.15	NS
BCS change	–.93	–.75	–.88	–.62	0.12	NS
			(kg)			
Cow initial weight	582.1	578.4	590.3	596.4	12.3	NS
Cow final weight	491.2	500.4	524.1	530.3	8.19	1, 2
Cow weight change	–90.9	–78.0	–66.2	-66.0	11.8	NS
Calf initial weight	170.9	168.7	175.9	163.4	5.12	NS
Calf final weight	191.6	195.8	202.3	192.7	5.17	NS
Calf weight gain	20.7	27.1	26.4	29.3	3.71	NS
24-hr milk production	2.87	3.21	3.43	5.22	0.58	NS

[1]SE, Standard error of the mean.
[2]Contrasts: 1, control vs. supplemented treatments; 2, energy vs. degraded intake protein + degraded intake protein undegraded intake protein combination; 3, degraded intake protein vs. degraded intake protein undegraded intake protein combination.
[3]NS, Not significant (P>0.10).

Table 10. Forage intake, total intake, forage intake as a percentage of body weight, and total intake as a percentage of body weight in Trial 2.

Item	Treatment				SE[1]	Contrast[2]
	Control	Energy	Degraded intake protein (DIP)	Degraded intake protein + undegraded intake protein (UIP)		
Forage intake (kg organic matter day^{-1})	13.5	14.0	16.5	14.7	0.80	NS
Total intake (kg organic matter day^{-1})	13.5	14.4	17.0	15.2	0.80	1
Forage intake (kg/100 kg body $weight^{-1}$ day^{-1})	2.68	2.62	3.04	2.67	0.16	NS
Total intake (kg/100 kg body $weight^{-1}$ day^{-1})	2.67	2.71	3.13	2.77	0.16	NS

[1]SE, Standard error of the mean.
[2]Contrasts: 1, control vs. supplemented treatments; 2, energy vs. degraded intake protein + degraded intake protein undegraded intake protein combination; 3, degraded intake protein vs. degraded intake protein undegraded intake protein combination.
NS, Not significant (P>0.10).

Forage intake and total intake (forage plus supplement; kg/100 kg body weight) was higher (P = 0.03) in 1994 compared to 1995 (3.0 vs 2.5 kg/100 kg body weight and 3.1 vs 2.6 kg/100 kg body weight). Cold temperatures likely reduced intakes in 1995 (Adams et al. 1986). However, based on the in vitro organic matter digestibility, we expected higher intakes in 1995 because forage quality was higher (Table 8).

The need for supplemental degraded intake protein (DIP) was underestimated in years 1 and 2 and the DIP + undegraded intake protein (UIP) protein combination supplement failed to supply adequate DIP. We estimated the requirement for DIP to be 547 g. However, in years 1 and 2, the DIP + UIP supplement only supplied 416 g DIP. Consequently, supplement formulations were changed in year 3 (Table 2). In year 3, the DIP +UIP supplement was formulated to supply 547 g DIP. The implication of underfeeding DIP while supplying excess UIP is unclear. No improvement in cow or calf performance was noted, as evidenced by the lack of a significant year by treatment interaction for body condition score change (P > 0.15) cow weight gain (P > 0.50), or calf weight gain (P > 0.50). Ruminants recycle nitrogen (NRC 1996); consequently, excess UIP could potentially substitute for DIP. The fact that cows perform similarly when supplemented daily or 3 times weekly indicates that recycling is important in production settings (Beaty et al. 1994).

Diets collected from esophageally cannulated cows averaged 6.2% crude protein, 1.2% UIP, and 52% in vitro organic matter digestibility during Trial 2. Crude protein was higher while UIP and digestibility were lower than we had estimated when supplements were formulated.

No differences were detected among treatments for cow weight change, cow body condition score change, or calf weight gain during the late lactation period (Table 9). Cow final weights were lower for control cows compared to cows receiving a supplement (P = 0.05). Cows receiving the energy supplement had lower final weights compared to protein supplemented cows (P = 0.06). Cows on all treatments lost body weight over the 70-day period. Average weight loss for the late lactation period was 75 kg. Large weight losses during late lactation are a concern; however, summer calving cows in this herd have access to vegetative forage for at least 30 days before calving and increases in body condition score to a score of 6 (on a 9 point scale) are common. Large loss of body condition could negatively impact winter performance of cows post weaning, because thin cows are likely to have higher maintenance requirements (Thompson et al. 1983).

Milk production tended (P = 0.12) to be higher for cows receiving the degraded intake protein degraded intake protein (DIP) + undegraded intake protein undegraded intake protein (UIP) supplement compared to the DIP. This is in agreement with the work of Lee et al. (1985) and Hibberd et al. (1988). No differences in milk production were reported when primiparous crossbred 2-year-old cows were fed 8.8% CP meadow hay and received either no supplement or 0.5 kg of a 40% CP soybean meal based supplement (Farthing 1993). Calf weight gain was not different among treatments.

No differences among treatments were detected (P > 0.17) for forage intake, forage intake as a percentage of body weight, and total intake as a percentage of body weight (Table 10). Total intake (kg/d) was higher for supplemented cows compared to the control (P < 0.10). No difference in hay intake by non-supplemented and supplemented primiparous cows were fed subirrigated meadow hay averaging 8.8% CP (Farthing 1993).

Again, the fact that cows did not respond to undegraded intake protein (UIP) in addition to degraded intake protein (DIP) may be due to the fact that estimated metabolizable protein requirement was too high, because milk production of the cows was overestimated. In addition, measured intakes were higher than expected, resulting in greater supply of metabolizable protein than expected. Based on average body weights, milk production, intake, digestibility, and protein degradability measured during Trial 2, the metabolizable protein requirement was 626 g and the metabolizable protein supply was 626 g. A response to additional UIP would not be expected based on this metabolizable protein requirement and supply.

Conclusions

Degraded intake protein was the first limiting nutrient before undegraded intake protein (UIP) and energy for summer calving cows grazing native range during the breeding season and late lactation. Supplementation with degraded intake protein (DIP) protein resulted in decreased weight and condition score losses during the autumn and winter periods. Calf gains were increased due to higher milk production during the autumn. Protein supplements such as alfalfa (*Medicago sativa* L.), soybean [*Glycine max* (L.) Merr.] meal, sunflower (*Helianthus annuus* L.) meal, or steep liquor, which are relatively high in degradability, are readily accessible for producers in the Nebraska Sandhills and can meet the supplemental protein requirements of summer calving cows during the breeding season and late lactation. Accurate estimates of milk production, intake, digestibility, and protein degradability are necessary to formulate supplements for grazing beef cattle based on DIP and metabolizable protein.

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Group size effects on grazing behaviour and efficiency in sheep

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Abstract

Two grazing trials were conducted during early winter (January 1996) and spring (April 1996) to evaluate the effect of group size on grazing efficiency and behaviour of sheep. Three treatments were tested, large (LG), medium (MG) and small group size (SG), with 2 replicates for each treatment of 12, 9, and 6 ewes, respectively. Groups were homogeneous for age and weight. Paddock size furnished 10 m^2 per sheep per day. Group size did not affect grazing efficiency and herbage intake in the winter, but in the spring, when herbage mass was more plentiful, the ewes in the small groups grazed shorter, had a lower herbage intake and a less efficient use of forage. Consequently, the sheep in the small groups gained less weight than those in the large groups in spring. Neither group size nor seasonal changes in forage quantity or quality influenced sheep selectivity. These results suggest that the choice of a proper flock size at pasture can play a major role in optimizing grazing efficiency in sheep, especially when feeding is largely based on grazing, as generally occurs in countries of the Mediterranean basin in spring. Under the conditions of this study, our results indicate that a flock size of more than 6 sheep should be used for studies on sheep grazing behaviour.

Key Words: diet quality, grazing management, intake

Grazing plays a major role in sheep feeding. Understanding the factors that affect sheep grazing behaviour and grazing efficiency may reduce feeding costs and improve sheep growth rate and reproductive performance. The ingestive behaviour of grazing sheep is seasonally affected by several factors including the animal's endocrine and metabolic state and the effects of climate on forage quality and quantity (Lynch et al. 1992). Stocking rate and flock size may also influence grazing behaviour and feed intake, because sheep are social animals (Rook and Penning 1991; Penning et al. 1993; Scott et al. 1996) and because they are selective grazers (Forbes, 1995). Selectivity is related to the number of grazing sheep and the amount of available herbage, i.e. grazing pressure (Lynch et al. 1992).

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Resumen

Se condujeron dos ensayos de apacentamiento durante el inico del inviero (Enero de 1996) y primavera (Abril de 1996) para evaluar el efecto del tamaño de grupo en el comportamiento y eficiencia de apacentamiento de ovinos. Se probaron tres tratmientos, grupo grande (LG), grupo mediano (MG) y grupo pequeño (SG) con dos repeticiones por tratamiento de 12, 9, y 6 borregas respectivamente. Los grupos eran homogénos en cuanto edad y peso. De acuerdo con el tamaño de potrero a cada borrego se asignaban 10 m^2 diarios. En invieron, el tamaño del grupo no afectó ni la eficiencia de apacentamiento ni el consumode forraje; sin embargo, en primavera cuando hubó más forraje disponible las borregas de los grupos pequeños apacentaron menos, tuvieron más bajo consumo de forraje y menos eficiencia del uso de forraje. Consecuentemente, en primavera, los borregos de los grupos pequeños ganaron menos peso que los de los gupos grandes. La selectividad de los borregos no fue influenciada ni por el tamaño de grupo ni por los cambios estacionales de calidad y cantidad de forraje. Estos resultados sugieren que la elección de un tamaño adecuado de rebaño puede jugar un papel importante en la optimización de la eficiencia de apacentamiento de los borregos, especialmente cuando la alimentacion es basada en apacentamiento, como generalmente ocurre en primavera en paises de la cuenca del Mediterráneo. Bajo las condiciones de este estudio, nuestros resutados indican que un rebaño de más de 6 borregos debe ser utilizado para estudios de comportamiento de apacentamiento de borregos.

Several authors have assessed the effect of stocking rate on sheep grazing efficiency and behaviour relative to grazing duration (Heitschmidt and Walker 1983, Sharrow 1983; Stoltz and Danckwerts, 1990; Ali and Sharrow, 1994), sward characteristics (Penning et al. 1991), season (Birrell 1991) and shape of paddock (Lynch and Hedges, 1979). Little is known about the effects of group size on sheep grazing behaviour. In flocks ranging from 1 to 15 ewes Penning et al. (1993) found reduced grazing times in small flocks, assuming that sheep in larger groups may benefit from social facilitation and/or from the increased number of individuals that are vigilant. There is little information on the effect of flock size on sheep grazing efficiency and behaviour or the influences of seasonal climatic effects or pasture conditions. The purpose of this study was to investigate the effects of group size on sheep grazing efficiency and behaviour during the winter and the spring seasons.

Materials and Methods

The experimental site was approximately 30 kilometers northeast of Foggia, Apulia, Southern Italy (latitude: 41° 27' 6" and longitude: 15° 33' 5"), with an elevation of about 100 metres above sea level. The climate of this area is Mediterranean, with about 500 mm of annual rainfall, mainly distributed in late autumn and winter, and a 22.1°C mean maximum temperature (often over 30°C from June to August). Rainfall, temperature, humidity, sun radiation, wind speed, and daily sunshine hours, were recorded throughout the trials at the meteorological station of the Capitanata Land-Reclamation Syndicate, about 0.5 km away from the site of experiment (Table 1). The area is covered by quaternary and recent alluvial soils. Sandy-silicious and alluvial soils are prevalent (24% and 21%, respectively), followed by clayey-calcareous soils (16%), calcretes (15%) and clayey-silicious soils (10%). The study pasture was composed of Graminaceae predominantly (*Lolium* spp., *Festuca* spp.) and to a smaller extent of Cruciferae, Compositae (*Carduus* spp.) and Leguminosae (*Trifolium* spp.). The above mentioned botanical families and genera were nearly always distributed in very complex mixes.

Grazing trials were conducted during early winter (January 1996) and spring (April 1996), and 54 dry Comisana ewes were used in each trial. Both trials lasted 30 days with each divided into three, 10-day grazing periods. Trials were preceded by a 7-day acclimation period so ewes could become acquainted with their peers. During this period the sheep grazed similar paddocks, adjacent to the experimental pastures. All ewes were familiar with forage found in pastures.

Three group sizes were tested, large group (LG, n=12) vs medium group (MG, n=9) vs small group (SG, n=6), with 2 replicates for each treatment. The ewes of the experimental groups were homogeneous for age (approximately 3 years) and weight (58 kg on average).

Table 1. Climatic data recorded throughout winter (January 1996) and spring (April) 1996 trials.

	Winter			Spring		
	Min	Max	Mean	Min	Max	Mean
Rainfall (mm/day)	0	15.6	3.5	0	5.6	1.3
Temperature (°C)	0.4	9.8	5.1	7.2	23.7	15.5
Humdity (%)	67.1	92.3	79.7	39.4	82.5	60.9
Sun radiation (W/m^2)	9.5	89.3	60.6	41.1	281.4	208.2
Wind speed (m/s)	0.58	5.11	2.89	1.25	6.08	2.92
Daily sunshine hours (n)	9.17	9.51	9.28	13.55	14.52	14.07

Paddock size was varied among treatments (60m x 20m, 50m x 18m, and 43m x 14m for LG, MG, and SG groups, respectively) to maintain a constant stocking rate of 10 m^2 per sheep per day. On average, daily forage allowance was 1.35, 1.39, and 1.36 kg DM/ewe/day in the winter and 1.89, 1.90 and 1.92 kg DM/ewe/day in the spring for LG, MG and SG treatments, respectively. Herbage composition was similar among the experimental groups. Paddocks were contiguous with mesh-fence boundaries. The groups of animals were somewhat isolated visually by rows of olive trees. Every day the ewes grazed from 09:00 hours to 17:00 hours with the rest of the day spent in separate straw-bedded pens. When the ewes returned to their own pens they were given vetch/oat hay (1.0 kg in winter and 0.5 kg in spring per head) and barley (0.25 kg per head in winter).

Measurements

Forage mass and composition was determined before and after each grazing period (10 days) by harvesting all herbage within 8 randomly selected 1 m^2 quadrates to ground level in all paddocks. Samples were dried in an oven at 50°C for 48 hours before weights were recorded. Herbage samples, as well as hay and barley (Table 2), were analysed for fat, crude protein, crude fibre, and ash (AOAC 1984). Average daily forage and nutrient intake was calculated as the difference between pre-grazing and post-grazing forage mass divided by ewe number x grazing period duration. Post-grazing forage mass was adjusted for growth during each period using estimates of pasture growth derived from cutting 8 randomly selected 1 m^2 quadrates in adjacent ungrazed pasture at the beginning and the end of each grazing period. Pasture utilisation efficiency was calculated as the ratio between forage intake and forage availability. The live-weights of the ewes were recorded at the beginning of the trial and subsequently every 10 days.

The grazing behaviour of the ewes was recorded by 3 trained observers equipped with video cameras on the 3rd, 6th and 9th day of each grazing period. Behavioural observations were conducted from 09:00 hours to17:00 hours and were divided into 60 min periods for each group. A different focal animal was chosen at random every day in each group and the 60 min observation periods were systematically rotated among treatments and replicates. Times spent eating, ruminating, standing inactive, resting, walking, defecating and urinating, exploring, and in other activities (self-grooming, grooming, scratching oneself, bleating, fencing biting) were recorded.

Table 2. Chemical composition and nutritive value of hay, barley and herbage.

	Vetch/oat hay	Barley	Herbage	
			Winter	Sping
Dry matter (%)	83.4	88.1	22.5	21.2
Crude protein (% DM)	14.1	12.7	16.9	19.1
Fat, by ether extract (% DM)	1.8	2.2	3.3	3.6
Crude fibre (% DM)	31.0	5.6	25.1	22.0
Ash (% DM)	9.1	2.7	10.1	10.2
N-free extract (% DM)	44.0	76.8	44.6	45.1
Gross energy (MJ/kg DM)	18.4†	18.6††	18.7†	20.3††

†Evaluated according to the equation by Lanari et al. (1993). ††Evaluated according to the equation by Schiemann et al. (1971).

Table 3. Estimated feed and nutrient intake and pasture utilisation efficiency (PUE) for large, medium and small groups in the winter and the spring trials.

	From herbage						From the supplements	
	Winter			Spring			Winter	Spring
	LG	MG	SG	LG	MG	SG		
DM intake								
(kg ewe/day)	0.75±0.lc	0.73±0.lc	0.71±0.lc	1.32±0.la	1.24±0.la	1.08±0. lb	1.05	0.42
Crude protein intake								
(g/ewe/day)	1 50.0±3.2c	147.5±2.7c	146.3±2.8c	286.4±3.0a	274.0±3.5a	240.8±2.9b	145.6	58.8
(% on DM)	20.0±0.5	20.2±0.4	20.6±0.5	21.7±0.4	22.1±0.3	22.3±0.5		
Fat intake								
(g/ewe/day)	24.0±0.3b	26.3±0.3b	27.0±0.4b	50.2±0.4a	49.6±0.4a	43.2±0.4a	19.9	7.5
(% onDM)	3.2±0.1	3.6±0.1	3.8±0.1	3.8±0.1	4.0±0.2	4.0±0.1		
Crude fibre intake								
(g/ewe/day)	155.3±3. 1c	151.1±1 .7c	144.8±2.4c	250.8±4. la	234.4±4.2a	200.9±3.8b	270.9	129.3
(% on DM)	20.7±0.2	20.7±0.3	20.4±0.2	19.0±0.4	18.9±0.4	18.6±0.5		
Ash intake								
(g/ewe/day)	78.8±1.7c	75.9±1.5c	74.6±1.8c	146.5±2.la	141.4±1.8a	121.0±1.9b	76.5	37.9
(% onDM)	10.5±0.2	10.4±0.2	10.5±0.2	11.1±0.3	11.4±0.2	11.2±0.2		
Gross energy								
(MJ/ewe/day)t	19.6±0.3c	19.6±0.4c	19.6±0.4c	21.3±0.3a	21.2±0.3a	20.7±0.4b	19.4	7.7
PUE (%)	55.6±2.lc	52.5±l.6c	52.2±l.6c	69.8±1.4a	65.3±1.8a	56.3±1.5b		

[t] Evaluated according to the equation by Lanari et aL (1993). Means within the same line followed by different letters are significantly different at P<0.05.

Statistical Analysis

Pasture and behavioural variables were subjected to analysis of variance for repeated measures (SAS 1990) and the following model was adopted: $y_{ijklm} = \mu + \alpha_i + \beta_{ij} + \chi_k + \delta_l + (\alpha\chi)_{ik} + (\alpha\delta)_{il} + (\chi\delta)_{kl} + (\alpha\chi\delta)_{ikl} + \varepsilon_{ijklm}$ where: γ_{ijklm} = experimental observation; μ = overall mean; α_i = group size; β_{ij} = replicate within group size; χ_k = season; δ_l = day of observation; $(\alpha\chi)_{ik}$ $(\alpha\delta)_{il}$ $(\chi\delta)_{kl}$ and $(\alpha\chi\delta)_{ikl}$ = interactions; ε_{ijklm} = random error. Group size, season and group size by season were sources of variation for the body weight and body weight changes of the ewes. When significant effects were found, the Student T test was used to locate significant (P<0.05) differences between means.

Results and Discussion

The data on herbage intake and pasture utilisation efficiency are reported in Table 3. Dry matter and nutrient intakes were higher in the spring than in the winter, depending on quantitative and qualitative supplement characteristics offered at each season (Avondo et al. 1995) and less on seasonal changes of herbage allowance and composition (Forbes 1995).

Group size did not affect herbage intake and pasture utilisation efficiency in the winter, but in the spring the ewes in the small groups had significantly smaller herbage and nutrient intakes and a lower pasture utilisation efficiency than the ewes in the medium and large groups. Based on measurements of changes in sward surface height, Penning et al. (1993) also reported a negative effect of small group sizes on herbage intake of sheep. Our results indicate that seasonal differences in level of supplementation and in herbage availability can play a major role in highlighting such differences of herbage intake.

Neither group size nor seasonal changes in pasture conditions seemed to have a direct effect on diet selection. Differential feed supplementation given to sheep in pens might partially account for the lack of shift in selectivity as well as for differences of herbage intake at pasture between the winter and the spring seasons (Jarrige 1988).

In both trials, grazing sheep spent a large part of the time (about 55 to 70%) eating (Table 4). Throughout the winter trial, eating times were similar among

Table 4. Grazing behaviour of large, medium and sm,all groups in the winter and the spring trials.

		Winter			Spring		
		LG	MG	SG	LG	MG	SG
Eating	(mm/day)	273.1±8.4b	275.0±7.7b	271.8±7.6b	334.0±8.la	303.2±8.4a	286.5±7.9b
Ruminating	(mm/day)	22.1±1.7	20.4±0.6	19.3±1.2	23.6±1.1	28.8±1.3	21.5±0.9
Standing	(mm/day)	28.1±2.3	27.6±1.4	28.2±1.3	27.2±0.9	29.2±1.2	26.8±1.0
Resting	(mm/day)	85.5±2.la	77.4±1.8ab	44.7±1.9c	58.9±1.4b	52.1±1.1b	40.1±1.3c
Walking	(mm/day)	38.8±1.7b	36.1±0.9b	57.0±1.4a	10.8±l.lc	24.7±0.9bc	56.8±1.2a
Defecat.+urinat.	(mm/day)	12.4±1.5	14.0±1.1	8.1±1.2	7.9±0.9	13.2±0.9	5.2±0.5
Exploring	(mm/day)	9.6±1.7b	14.1±1.lb	35.8±1.3a	6.3±0.6b	13.2±0.8b	33.3±0.9a
Otheractivities	(mm/day)	10.4±1.1	15.4±2.0	15.1±0.9	11.3±0.7	15.6±1.1	9.8±0.7

Means within the same line followed by different letters are signilicantly different at P<0.05.

Table 5. Body weight changes (BWC) of the ewes in large, medium, and small groups in the winter and the spring trials.

		Winter			Spring		
		LG	MG	SG	LG	MG	SG
Initial body weight	(kg)	57.30±1.4	58.01±1.4	58.83±1.2	58.06±1.6	58.21±1.5	57.63±1.6
Finalbodyweight	(kg)	57.63±1.6	58.17±1.1	58.68±0.9	58.96±1.4	58.81±1.4	57.81±1.2
BWC	(g/d)	11.1±0.lab	5.2±0.1b	-5.1±0.1	30.1±0.la	19.9±0.lab	6.1±0.2b

Means within the same line followed by different letters are significantly different at P.<0.05.

the treatments, while in spring the SG ewes exhibited markedly lower eating times than the large group (LG) and the medium group (MG) ones. These results matched the differences observed for herbage intake among the groups. In both trials, the ewes in the small groups spent less time resting and differences were more evident in winter. Overall, resting times were higher in the winter season, resting close together presumably is for thermoregulatory purposes. Time spent walking and exploring was higher in the small than in the large and medium groups; walking took a longer time in the winter than in the spring season, too. According to Penning et al. (1993), the longer time spent in exploratory behaviour by the ewes in the small groups might be ascribed to an ancestral behaviour correlated with the level of perceived danger of predation. Security may be derived from the increased number of sheep that are vigilant in larger groups (Pulliam 1973). In addition, the less effective social exploration the smaller the group (Fraser and Broom 1990) and since animals give a very high priority to exploration, it is not surprising that such behaviour may steal time also from feeding activity. The stronger kinetic drive of ewes in small groups to investigate the environment might be responsible for their increased locomotion (Carson 1985). Differences of time spent walking during winter and spring trials might be attributed to changes in herbage allowance or quality. Walking, which is part of searching behaviour (Gluesing and Balph 1980), may also be affected by availability and location of food (Fraser and Broom 1990). Due to less energy intake and/or a greater loss of energy form walking or exploring, the ewes in the small groups gained less weight than those in the medium and large groups in the spring (Table 5).

Management Implications

McClymont (1967) reported social facilitation of feeding behaviour in sheep and Southcott et al. (1962) found that animals maintained in smaller group sizes gained less weight than those maintained in larger group sizes. More recently Penning et al. (1993) observed that sheep in small groups spent less time grazing than those in large groups and that animals in groups of 1 or 2 tended to have shorter meals than those in groups of 3 to 15, assuming a reduced intake of herbage in groups of less than 4 sheep, too. Our results confirm previous findings and hypotheses, adding further information about the factors affecting herbage intake in flocks of different group sizes. First, our results suggest that both pasture conditions and level of supplementation must be taken in account to evaluate correctly the effect of group size on sheep feeding behaviour at pasture; in fact, differences in grazing time, pasture utilisation efficiency, herbage intake and body weight changes were small and not significant in the winter, whereas they were more evidently in favour of medium and large groups in the spring, when sheep feeding was largely based on grazing. In both trials, but especially in the spring, the ewes in the small groups spent more time in alternative behaviours, such as walking and exploring, to ingestive activity detriment, and this resulted not only in a reduced herbage intake but also in a greater waste of energy, both perhaps responsible for reduced weight gains. Hence, the importance of social facilitation for feeding at pasture in sheep is confirmed. Under the conditions of this study the existence of a group size effect on grazing behaviour of sheep also for groups of more than 4 animals is demonstrated. Thus, our results clearly indicate that flock size at pasture may be a critical variable in determining grazing behaviour and efficiency of sheep, especially when feeding is largely based on grazing, as generally occurs in countries of the Mediterranean basin in spring. Our findings also indicate that a minimum flock size of more than 6 sheep is required for studies that are investigating grazing time and intake of sheep.

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Cattle grazing and avian communities of the St. Lawrence River Islands

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Abstract

Three hundred islands are found along the St. Lawrence River in Québec. Among these islands, over 5,000 ha are used for agricultural purposes and 32% of this total is devoted to communal pasture, a traditional practice in this part of the river. In 1993 and 1994, we compared the avian communities of 500 ha natural spring flooded prairie islands subjected to different degrees of grazing pressure. Three islands were divided into 12 sectors, in which 108 sample plots of 0.5 ha were selected. Results show that the degree of visual obstruction by herbaceous vegetation and the percentage of shrub cover were higher on ungrazed and on moderately grazed prairie (<1 cow/ha/year) as compared with intensively grazed prairie (>1 cow/ha/year). More than 1,650 observations of passerines were made and 13 species were identified. The Swamp Sparrow (*Melospiza georgiana*), Savannah Sparrow (*Passerculus sandwichensis*), Red-winged Blackbird (*Agelais phoeniceus*), and Bobolink (*Dolichonyx oryzivorus*) were the 4 most abundant species, accounting for over 80% of all birds counted. Ungrazed and moderately grazed prairie contained 6 times more birds than intensively grazed prairie (10.4 birds/ha and 11.7 birds/ha vs 1.6 birds/ha). We also recorded 167 and 113 dabbling duck (anatinae) nests in 1993 and 1994 respectively. Moderately grazed and ungrazed prairies had a nest density nearly 10 times higher than that of intensively grazed prairie (0.50 ± 0.01 and 0.30 ± 0.0 1 nest/ha vs 0.05 ± 0.01 nest/ha). Our study shows that grazing pressure on prairies of the studied islands largely determined the type of bird species present. However, prairie subjected to excessive grazing pressure is not suitable for waterfowl nesting. Various recommendations are provided for integrated management of wildlife and agriculture on the St. Lawrence River communal pasture islands.

Resumen

A lo largo del río St. Lawrence en Québec se encuentran trecientas islas. En estas islas más de 5,000 ha son utilizadas con fines agrícolas y 32% de este total se dedica a actividades comunales de apacentamiento la cual es una práctica común en esta parte del río. En 1993 y 1994 comparamos las comunidades de aves en 500 ha de praderas isleñas sujetas a diferentes grados de presión de apacentamiento. Tres islas se dividieron en tres sectores, en los cuales se seleccionaron 108 parcelas de muestreo de 0.5 ha. Los resultados muestran que el grado de obstrucción visual por vegetación herbácea y el porcentaje de cobertura de arbustos fueron mayores en praderas sin apacentamiento o que recibieron apacentamiento moderado (<1 vaca por año) que en las que fueron apacentadas intensivamente (>1 vaca por año). Se hicieron más de 1650 observaciones y se identificaron 13 especies.. El "Swamp sparrow" (*Melospiza georgiana*), "Savannah sparrow" (*Passerculus sandwichensis*), "Redwinged blackbird" (*Agelais phoeniceusi*) y "Bobolink" (*Dolichonyx oryzivorus*) fueron las cuatro especies más abundantes y comprendieron más del 80% del total de aves contadas Las praderas sin apacentamiento o apacentadas moderadamente tuvieron 6 veces más aves que las praderas apacentadas intensivamente (10.4 y 11.7 aves /ha vs 1.6 aves/ha). En 1993 y 1994 registramos 167 y 113 nidos de "Dabblin duck" (anatinae) En las praderas sin apacentamiento o con apacentamiento moderado la densidad de nidos fue casi 10 veces mayor que en las praderas apacentadas intensivamente (0.5 ± 0.01 y 0.30 ± 0.01 nidos/ha vs 0.05 ± 0.01 nidos/ha) Nuestro estudio muestra que la presión de apacentamiento en las praderas de las islas estudiadas determina en gran medida el tipo de especie de aves presentes en estas praderas. Sin embargo, las praderas sujetas a una presión de apacentamiento excesiva no son apropiadas para el anidamiento del "Waterfowl'. Se proveen varias recomendaciones para un manejo integrado de la fauna silvestre y agricultura para la praderas comunales de las islas del río St. Lawrence.

Key Words: agriculture, birds, livestock, pasture, flooded prairies, Québec, waterfowl

Along the St. Lawrence River in Québec there are many archipelagos, individually numbering over 300 islands. Over 5,000 ha of their area is used for agricultural purposes, with 32% (1,685 ha) of this total devoted to communal pasture, a

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traditional practice in this part of the river (De Koninck 1970, Pilon et al. 1981). Islands have been used as communal pasturelands by local farmers for many decades. Year-to-year, cows are brought over by a flat boat in late May or early June and taken back in mid-November. In recent years, major efforts have been made to increase our knowledge of the potential of these islands for wildlife and to devise various strategies for conserving biodiversity (Bélanger and Lehoux 1995).

Because it modifies both plant species composition and abundance, livestock grazing reduces the richness and density of avian communities that use western prairie habitat (Kirsch et al. 1978, Kantrud 1981, Taylor 1986, Bowen and Kruse 1993). It also has been shown that waterfowl nest density and nesting success are significantly reduced in grazed prairies (Glover 1956, Kirsh 1969, Higgins 1977, Kirsh et al. 1978, Klett et al. 1988, Kirby et al. 1992). However, the impact of livestock grazing in the eastern part of this continent, where the type of herbaceous natural prairie, herd management and bird populations differ, has not been studied.

The objective of our study was to compare the avian communities of natural spring flooded prairie of the St. Lawrence River islands subjected to different degrees of grazing pressure, to provide recommendations for integrated wildlife and range management.

Study Areas and Methods

Our study was carried out on 3 islands of the Berthier-Sorel archhipelago located less than 100 km east of Montréal, namely Moine, Barques and Ronde islands. Moine Island has an area of nearly 590 ha, of which over 50% (307 ha) is covered by natural spring flooded herbaceous prairie dominated by reed canary grass (*Phalaris arundinacea*)(Marie-Victorin 1964) (Table 1). Although there are a few old wire fences that divide the island into different rough pasture units, they are obviously ineffective since livestock can easily get around them. Hence, more than 100 cows move freely around the island. Barques Island has a total area of nearly 175 ha, with herbaceous prairie covering approximately 70%, or 123 ha. Although reed canary grass is predominant, common reed grass (*Phragmites communis*) has grown extensively on dredge spoil deposited on the island when the St. Lawrence Seaway was created. Livestock was present about 30 years ago, but this island has not been used for agriculture since that time. Ronde Island has an area of about 30 ha. More than 50 animals (cows and sheep) graze from early May to late October; hence, the vegetation cover is heavily degraded. Herbaceous prairie covers more than 95% of the island. In this paper, the avian communities of natural prairie (ungrazed), moderately grazed prairie (<1 cow/ha/year) and intensively grazed prairie (>1 cow/ha/year) were compared.

Description of the vegetation cover and bird surveys

The 3 islands were subdivided into 20 sectors, each consisting of 100 ha, according to the map mercator system (UTM). A grid made up of 0.5 ha units was then superimposed, and 108 sample plots were selected. Although distributed in proportion to the respective area of the islands, the plots were nonetheless selected randomly within each island. This approach yielded 68 sampling plots on Moine Island, 30 on Barques Island and 10 on Ronde Island. Consequently, 11%, 12% and 8% respectively, of the total area of herbaceous prairie of these islands was surveyed.

Vegetation surveys were carried out in late May and early June 1993 in all the plots. A sampling station was positioned every 10 m along a diagonal line crossing each plot from east to west, for a maximum of 10 measurements/plot. At each station, we noted the dominant and co-dominant plant species within a 1 m^2, the degree of visual obstruction associated with the herbaceous vegetation cover (Robel et al. 1970), and the percentage of shrub cover.

The same 108 plots were used in 1993 to conduct a survey of passerine birds following Bibby et al. (1992). A count was done within each plot as follows: the observer walked slowly, noting the position, species and sex, if possible, of all birds seen or heard. Upon reaching the middle of the plot, the observer listened for 5 minutes and then walked to the far end of the plot. It took the observer approximately 10 minutes to cover each plot. Sampling was conducted during the first 2 weeks of June. Bird counts were done between sunrise (0500 hours) and 1000 hours. Each plot was surveyed 5 times.

A duck nest survey was carried out in 1993 between mid-May and early July. This survey encompassed the entire area of herbaceous prairie on each island and was done 3 times. In the common reed grass communities on Barques Island, only the immediate periphery of the stand was surveyed, due to the excessive density of stems and the low probability of finding nests. The census and nest description procedures used follow recommendations of Klett et al. (1986). The counts were generally done between 0800 and 1400 hours (Gloutney et al. 1993), although the nest searching sometimes had to be continued until 1600 hours. Four to 12 persons walked abreast, beating the vegetation to flush hens from nests. Whenever a nest was found, the number of eggs present was noted and their incubation stage was determined by the flotation method (Klett et al. 1986). A description was

Table 1. Survey efforts and characteristics of the studied prairie habitats on 3 St. Lawrence River communal pasture islands, Québec, 1993–1994.

	Moine Island	Barques Island	Ronde Island
Grazing regime category	moderate	none	intensive
Cow density (animal units)	≤ 1 cow/ha/year	0 /ha/year	> 1 cow /ha/year
Total area of the island	590 ha	175 ha	70 ha
Area (%) of the island covered by herbaceous prairie	307 ha (52.03%)	123 ha (70.29%)	67 ha (95.71%)
Area of the surveyed sectors	270 ha	120 ha	60 ha
Area (%) of herbaceous prairie sampled	34 ha (11.1%)	15 ha (12.2%)	5 ha (7.5%)
Number of sample plots	68	30	10

Table 2. **Plant cover characteristics of the herbaceous prairie of 3 St.Lawrence River communal pasture islands, Québec, 1993–1994.**

Grazing Pressure	Obstruction	Shrub Cover
	(cm)	(%)
ungrazed	27.0 ± 0.6A	3.7 ± 0.4A
moderately grazed	24.5 ± 0.6A	2.2 ± 0.2B
intensively grazed	7.2 ± 0.5B	0.0 ± 0.0C

also made of the vegetation present in a 1 m^2 quadrat around the nest (used as a central point) by assigning a percentage of cover to the different plant species present. Various other measurements were taken, such as, visual obstruction by herbaceous vegetation cover (Robel et al. 1970) and the heights of the tallest living (annual or growing vegetation) and dead (litter or residual vegetation) stems. The exact position of the nests was marked on colour aerial photos (1:1,500) of the islands, and nest locations in the field were identified by installing a marker post 15 m to the northeast of each of them at a precise angle. The nests were visited a second time to record their fate.

In 1994, another nest count was conducted on Moine Island and Ronde Island to better document the nesting success of dabbling ducks on these unmanaged islands. In contrast with the previous year, the nest search was carried out using the rope dragging method (Klett et al. 1986), which consisted of pulling a weighted rope about 10 m long stretched between 2 motorcycles. A third person followed behind to locate the exact spot from which the hens flew and to identify the species involved. Landmarks along the shore, marker stakes and a compass were used to carefully delimit the areas surveyed in each count and to ensure coverage of all the prairie habitat on the islands. The same nest location and description procedures were employed as in 1993, except that to overcome the problem of livestock trampling and knocking down the posts used to mark nest locations, a radiotransmitter was placed underneath 40 nests randomly distributed on the islands, with the antenna extending beyond the nest. Each of these nests was visited every 7 days until its fate was determined.

Data analysis

The mean of the 10 measurements made in each plot was adopted as the evaluation of visual obstruction by herbaceous vegetation cover present. In addition, the coefficient of variation of this mean was used to document the degree of uniformity or homogeneity of the plant cover within each plot. For comparison purposes, the latter provides a better estimate than variance or the standard deviation because it is not affected by the value of the mean (Zar 1974).

In the case of the passerine bird counts, for each species, the day with the maximum number of records out of the 5 surveys conducted was used for subsequent comparisons between prairie types (Bibby et al. 1992). Hence, for each species and species group, the survey with the highest number of observations was selected. The selected day varied from 1 species to the next. Finally, the number of duck nests in each survey sector was determined by superimposing their boundaries on the colour aerial photos used in identifying the nest locations. The mean number of nests/island is actually the mean of nest density in each sector studied. A nest was considered as successful if at least 1 of the eggs had hatched. The nesting success of the different species was calculated in terms of apparent success (number of nests with hatched birds/total number of nests), and also by using a modified version of the Mayfield method (Klett et al. 1986) which takes into account the number of days the nest is exposed to predators.

Data analysis was conducted following Zar (1974), and by using the SAS program (SAS Inst. Inc, personal computer version). The vegetation characteristics were compared among sectors/islands through one-way analysis of variance followed by multiple comparison tests (SNK and Tukey). Simple Pearson correlation coefficients were used to compare relationships between the characteristics of the plant communities in the sampling sectors and, as applicable, the total density of duck nests or the abundance of passerines. An analysis of habitat selection by the different passerine species was conducted using the method of Neu et al. (1974). Finally, the standard error (SE) is given for all means presented in this text and in the tables. The probability level for statistical tests was set at 5% throughout the analyses.

Results

Characteristics of the vegetation cover

The degree of visual obstruction ($F = 89.4$, $df = 2$, $P<0.0001$) and the percentage of shrub cover ($F = 20.5$, $df = 2$, $P<0.0001$) differed among the 3 types of prairie (Table 2). In comparing the vegetation characteristics of various sectors surveyed on the 3 islands, a significant difference was also found in both the visual obstruction measure ($F = 59.0$, $df = 10$, $P<0.0001$) and the percentage of shrub cover ($F= 29.8$, $df = 10$, $P<0.0001$). Finally, the degree of homogeneity of the herbaceous plant cover also differed among the 3 islands studied ($F = 12.2$, $df = 2$, $P = 0.0001$).

Habitat use by passerine birds

A total of 540 counts was conducted, comprising 1,659 records of birds. In all, 13 passerine species were observed: 10 species on Moine Island, 11 on Barques Island and only 2 on Ronde Island (Table 3). The Savannah Sparrow (*Passerculus sandwichensis*) was the only species observed on all 3 islands. The 4 most common species, the Swamp Sparrow (*Melospiza georgiana;* n = 592) (Gauthier and Aubry 1995), Savannah Sparrow (n = 342), Red-winged Blackbird (*Agelaius phoeniceus;* n = 203) and Bobolink (*Dolichonyx oryzivorus*; n = 196), accounted for more than 80% of the observations. Sedge Wrens (*Cistothorus platensis*) were present on Barques Island while Sharp-tailed Sparrows (*Ammodramus caudacutus*) and Brown-headed Cowbirds (*Molothrus ater*) were found on Moine Island. The Eastern Meadowlark (*Sturnella magna*) was observed only once on Ronde Island.

The 13 species observed were divided into 5 groups based on certain taxonomical and ecological characteristics. The 4 sparrow species were grouped together in the sparrow group (TOTBRU), the 2 warbler species and the American Goldfinch (*Carduelis tristis*) in the war-

Table 3. Species composition (number of birds/species and relative abundance [%]) of passerines associated with wet meadows, according to 3 different levels of grazing on St. Lawrence communal pasture islands, Quebec.

Species	None (Barques 1.)		Grazing Pressure Moderate (Moine I.)		Intensive (Ronde I.)		Total
	(no)	(%)	(no)	(%)	(no)	(%)	(no)
Red-winged blackbird	39	(7.33)	164	(14.83)	0	(0.00)	203
American goldfinch	9	(1.69)	9	(0.81)	0	(0.00)	8
Yellow warbler	69	(12.97)	28	(2.53)	0	(0.00)	97
Common yellowthroat	49	(9.21)	57	(5.15)	0	(0.00)	106
Bobolink	21	(3.95)	175	(15.82)	0	(0.00)	196
Song sparrow	38	(7.14)	7	(0.63)	0	(0.00)	45
Swamp sparrow	239	(44.92)	353	(31.92)	0	(0.00)	592
Savannah sparrow	55	(10.34)	267	(24.14)	20	(95.00)	342
Sharp-tailed sparrow	0	(0.00)	13	(1.18)	0	(0.00)	13
Eastern meadowlark	0	(0.00)	0	(0.00)	1	(4.76)	1
Sedge wren	7	(1.32)	0	(0.00)	0	(0.00)	7
Marsh wren	6	(1.13)	29	(2.62)	0	(0.00)	35
Brown-headed cowbird	0	(0.00)	4	(0.36)	0	(0.00)	4

bler group (TOTWARB), and the 2 wren species in the wren group (TOTROG). The icterid group comprised Red-winged Blackbirds, Brown-headed Cowbirds and Eastern Meadowlarks (TOTICTE). Bobolinks (GOGL), although they are icterids, were analysed separately in view of their declining status in North America. The analysis of these 5 groups revealed significant differences in their abundance on the 3 islands under study ($x^2 = 136.9$, df = 8, P = 0.001) (Table 4). Even when paired, the significant differences mentioned earlier still existed between Barques Island and Moine Island ($x^2 = 124.1$, df = 4, P = 0.001), between Moine Island and Ronde Island ($x^2 = 12.1$, df = 4, P = 0.017) and between Barques Island and Ronde Island ($x^2 = 9.96$, df = 4, P = 0.041). The sparrow group was the largest group, mainly due to the high density of Swamp Sparrows on Moine and Barques islands. The minimum densities (all species combined) found were 10.4 birds/ha on Moine Island, 11.7 birds/ha on Barques Island and 1.6 birds/ha on Ronde Island. Thus, the ungrazed and the moderately grazed prairie had 6 times more birds than the intensively grazed prairie habitat.

An analysis of habitat selection was conducted for the different species groups (Table 5). Habitat availability was determined based on the number of plots found on each of the islands, since each plot had the same area and was surveyed 5 times in all; hence, the minimum number of observations was 54. Bobolinks, and icterids as a whole, preferred moderately grazed prairie and avoided ungrazed and intensively grazed prairie. Species in the warbler group preferred ungrazed natural prairie and shunned the other 2 types of prairie. Sparrows, too, preferred ungrazed prairie, but used moderately grazed prairie in the proportions present and avoided intensively grazed prairie. A significant difference was found between shrub cover on ungrazed and moderately grazed prairie. The wren group was not statistically analysed because of the insufficient number of observations (n = 42).

Habitat selection was then analysed for those species which had been observed in sufficient numbers. We found no significant difference between the number of birds observed on ungrazed and moderately grazed herbaceous prairie for the Common Yellowthroat, Swamp Sparrow, Marsh Wren, Savannah Sparrow, sparrows as a whole (TOTBRU), wrens as a whole (TOTROG) and passerines overall (Table 6). However, there were significantly more Red-winged Blackbirds,

Table 4. Maximum number of observations and bird densities found on each of the 3 islands studied in relation to the different grazing levels.

Species and Species Group	Moderate Grazing (Moine Island) Maximum	Density	No Grazing (Barques Island) Maximum	Density	Intensive Grazing (Ronde Island) Maximum	Density
	(no. obs.)	(no./ha)	(no. obs.)	(no./ha)	(no. obs.)	(no./ha)
Total No. of Birds	355	10.44	176	11.73	8	1.60
TOTBRU	187	5.50	103	6.87	7	1.40
GOGL	58	1.71	8	0.53	0	0.00
TOTICTE	60	1.76	14	0.93	0	0.20
TOTWARB	41	1.21	45	3.00	0	0.00
TOTROG	9	0.26	6	0. 40	0	0.00
Red-winged blackbird	57	1.68	14	0.93	0	0.00
American goldfinch	7	0.21	8	0.53	0	0.00
Yellow warbler	12	0.35	19	1.27	7	0.00
Common yellowthroat	22	0.65	18	1.20	0	0.00
Song sparrow	3	0.09	10	0.67	0	0.00
Swamp sparrow	103	3.03	74	4.93	0	0.00
Savannah sparrow	72	2.12	19	1.27	7	1.40
Sharp-tailed sparrow	9	0.26	0	0.00	0	0.00
Eastern meadowlark	0	0.00	0	0.00	1	0.20
Sedge wren	0	0.00	3	0.20	0	0.00
Marsh wren	9	0.26	3	0.20	0	0.00VA
Brown-headed cowbird	3	0.09	0	0.00	0	0.00

Table 5. Number of birds/species, relative importance (%) of groups of passerine species and degree of selection of herbaceous prairie according to 3 different levels of grazing (see Table 1) on St. Lawrence communal pasture islands, Quebec. For the meaning of the abbreviations, see text. The wren group was not analysed due to the extremely small number of them observed (n <54 records). A "–" sign denotes habitat avoidance, a "+" sign indicates habitat selection, and a "0" indicates that the habitat was neither preferred nor selected.

Species		Grazing Intensity		
Group	None	Moderate	Intensive	Total
	No. (%)	No. (%)	No. (%)	No
TOTBRU	332 (33.47) +	640 (64.52) 0	20 (2.02) –	992
GOGL	21 (10.71) –	175 (89.29) +	0 (0.00) –	196
TOTICTE	39 (18.75) –	168 (80.77) +	1 (0.48) –	208
TOTPARU	127 (57.47) +	94 (42.53) –	0 (0.00) –	221

Bobolinks, and icterids overall (TOTICTE) on moderately grazed prairie than on ungrazed prairie. Finally, there were significantly more Yellow Warblers, Song Sparrows, warblers overall (TOTWARB) and American Goldfinches on ungrazed prairie than on moderately grazed prairie.

The effect of the vegetation cover on the distribution of the different passerine species was also examined. The 2 variables considered (visual obstruction and shrub cover) were not significantly associated with total use of the habitat by passerines (Table 7). However, a significant positive association was found between the percentage of shrubs and the presence of American Goldfinches, Yellow Warblers and Song Sparrows; a positive correlation was also found between the degree of visual obstruction and the presence of Common Yellowthroats and Swamp Sparrows.

Waterfowl nesting and nesting success

In all, 167 dabbling duck nests were found on the 3 islands in 1993. This represents a density of 0.34 nests/ha, taking into account only the area of prairie habitat on the islands. More specifically, we found 129 nests on Moine Island, 36 on Barques Island and only two nests on Ronde Island. This is equivalent to densities of 0.50 ± 0.01, 0.30 ± 0.01 and 0.05 ± 0.01 nests/ha for moderately grazed, ungrazed and intensively grazed prairie, respectively (F = 135.7, df = 2, P<0.0001).

In 1993, the Northern Pintail (*Anas acuta*) (26%), Gadwall (*Anas strepera*) (31%) and Mallard (*Anas platyrynchos*) (17%) dominated the list of species censused. The Black Duck (*Anas rubripes*) accounted for only 1% of all nests found, whereas a total of 6 Blue-winged Teal (*Anas discors*) nests were found. The species composition of the nesting ducks was fairly similar for Moine Island and Barques Island, whereas the Northern Pintail was the only species found nesting on Ronde Island. Of the 167 nests counted in spring 1993, 67 were later revisited to determine their fate. Of these, only 11 had hatched eggs, for an apparent nesting success of about 16%. The apparent nesting success varied among the islands, from 22.9% (n = 48) on Moine Island to 0% on Barques Island (n = 18). The very small number of nests on Ronde Island made it difficult to assess this aspect of duck nesting ecology there.

In 1994, despite the use of a different census technique, similar results to those of 1993 were obtained: 113 nests were found on Moine Island, for a density of 0.39 nests/ha, and no nests were found on Ronde Island. The Gadwall, Northern Pintail and Mallard were still the dominant species but, however, the Northern Shoveler (*Anas clypeata*), made up 16% of the records. Once again, the Black Duck and the Blue-winged Teal accounted for only a small percentage of the nests found, 2 and 4% respectively. On Moine Island an apparent nesting success of 32.3% were calculated in 1994, compared with 22.9% in 1993. The apparent nesting success ranged from 20% for Mallards to 47% for Northern Shovelers. Using the modified Mayfield method, mean nesting success was 14.4% for all species combined, with a confidence interval ranging from 8.9 to 23.2%. Nesting success varied widely among the different species, from a low of 3.8% for Northern Pintails to a high of 30.7% for Northern Shovelers. Examining only those sectors for which the fate of at least 5 nests was known, we did not find any significant relationship between the ducks' apparent nesting success and the degree of visual obstruction by herbaceous vegetation cover (r = –0.44, p = 0.32) or shrub cover (r = –0.24, P = 0.60). However, the number of sectors considered was relatively low (n = 7) to shed much light on such relationships.

On the islands' prairie habitat, 86% of the surveyed nests were located in vegetation cover dominated by reed canary grass. Various sedge (3.0%) (*Carex* spp.) and goldenrod (1.1%) (*Solidago* spp.) species were the other dominant vegetation types found at nests. With respect to the main codominant species,

Table 6. Comparison of the mean (± SE) number of birds per sample plot for the survey with the maximum number of observations on 2 St. Lawrence communal pasture islands with different levels of grazing intensity, Quebec, 1993. The survey date may vary among the species and species groups. Only the species for which the total number of observations for both islands is >10 were retained.

Species/Group	Moderate Grazing	No Grazing	P
Red-winged blackbird	0.75 ± 1.06*	0.20 ± 0.48	0.0077
American goldfinch	0.03 ± 0.24	0.27 ± 0.69	0.0136
Yellow warbler	0.13 ± 0.38	0.53 ± 0.86	0.0018
Common yellowthroat	0.25 ± 0.74	0.40 ± 0.67	0.3451
Bobolink	0.68 ± 1.14*	0.20 ± 0.48	0.0302
Song sparrow	0.03 ± 0.17*	0.33 ± 0.92*	0.0098
Swamp sparrow	1.38 ± 1.64	1.90 ± 1.75	0.1613
Savannah sparrow	0.96 ± 1.49	0.37 ± 1.30	0.0642
TOTBRU	2.32 ± 2.11	2.30 ± 1.70	0.9571
TOTICTE	0.76 ± 1.09*	0.20 ± 0.48	0.0081
TOTWARB	0.41 ± 1.07*	1.20 ± 1.73*	0.0070
TOTROG	0.12 ± 0.51	0.10 ± 0.31	0.8595
Total No. of Passerines	3.82 ± 2.53	3.73 ± 2.23	0.8667

*Significant differences (P<O.05)

Table 7. Pearson correlation coefficients between the maximum number of birds/survey/plot and certain plant cover characteristics. For the latin names of the species or the meaning of the abbreviations see text.

Species or Species Group	Mean Visual Obstruction/Plot		Mean Shrub Cover/Plot	
	(r)	(p)	(r)	(p)
Total Number of Birds	0.37	0.12	0.24	0.32
TOTBRU	0.25	0.30	0.24	0.31
GOGL	0.43	0.07	-0.24	0.32
TOTICTE	0.22	0.36	-0.06	0.81
TOTPARU	0.29	0.22	0.52	0.02
TOTROG	0.35	0.15	-0.10	0.69
Red-winged blackbird	0.23	0.35	-0.10	0.68
American goldfinch	-0.11	0.66	0.52	0.02
Yellow warbler	0.14	0.55	0.68	0.002
Common yellowthroat	0.60	0.007	0.12	0.62
Song sparrow	-0.07	0.78	0.66	0.002
Swamp sparrow	0.57	0.01	0.11	0.66
Savannah sparrow	-0.37	0.12	0.03	0.91
Sharp-tailed sparrow	-0.14	0.57	-0.24	0.32
Eastern meadowlark	-0.34	0.15	-0.17	0.50
Sedge wren	0.18	0.47	-0.06	0.82
Marsh wren	0.31	0.19	-0.09	0.72
Brown-headed cowbird	0.23	0.35	0.36	0.13

the most common were horsetail species (40%) (*Equisetum* spp.), sedge species (18%) and bird vetch (14%) (*Vicia cracca*). The plant species composition differed little among the various duck species, with reed canary grass being the dominant plant in over 70% of cases. The mean height of growing vegetation was 62.0 ± 2.0 cm, compared with 27.9 ± 1.3 cm for litter. We obtained a mean visual obstruction measure of 49.8 ± 1.9 cm.

We related the variation in nest density to the degree of visual obstruction by vegetation. Mean nest density was associated with the obstruction measure ($r = 0.58$, $n = 19$, $P = 0.009$) but the mean percentage of shrubs was not associated with nest density ($r = 0.13$, $n = 19$, $P = 0.60$). It should be kept in mind, however, that shrub coverage varied little among the different sectors of the studied islands. No significant relationship was observed between the measure of the homogeneity of the vegetation cover, and nest density; however, there did appear to be a slight trend ($r = 0.38$, $n = 19$, $P = 0.108$).

Discussion

Use of prairie habitat by passerines

Various studies conducted in the western part of North America have shown that livestock grazing, since it modifies both plant species composition and abundance, reduces bird species richness and density of the avian communities of prairie habitat (Bowen and Kruse 1993). The species richness observed on the prairie habitats of the islands in this study is nonetheless lower than that reported in other studies done in western prairies (Owens and Myers 1973, Kantrud and Koligiski 1982, Zimmerman 1992). However, our results are fairly consistent with other eastern bird data since 11 to 18 species are generally observed on the herbaceous prairie of the islands along the St. Lawrence River (Pilon et al. 1981).

Intensively grazed prairie is shunned by most prairie-associated passerine birds. No species and no species group for which habitat selection was analysed showed a preference for the heavily grazed island. The diminished quality of plant cover resulting from intensive grazing leads to a decline in the number and diversity of bird species. Similar observations have been made elsewhere in North America (Kantrud 1981, Kirsh et al. 1978). With respect to the other types of prairie (ungrazed and moderately grazed), very few differences were noted in the species composition of the avian communities, although the relative importance of the various species and/or species groups differed significantly among them. Thus, livestock grazing on prairie habitats of the communal pasture islands of the St. Lawrence River largely determines the bird species that are present. For example, species in the warbler group preferred ungrazed prairie, as did sparrows, although the sparrow's preference was less pronounced. This muted preference may be related to the fact that some sparrows preferred ungrazed prairie (Swamp Sparrow), while others selected moderately grazed prairie (Savannah Sparrow). The Savannah Sparrow is known to avoid heavily grazed areas (Bock et al. 1993), although once established, it may return to the same site regardless of its nesting success (Bédard and Lapointe 1984).

The presence of shrubs and dense emergent reed beds (particularly cattails; *Typha* spp.) near temporary ponds in natural ungrazed prairie habitat on Barques Island is probably an important factor in the selection of this habitat by some bird species (the warbler group overall and the Swamp Sparrow). Song Sparrows also seemed to prefer ungrazed prairie, although the number of observations was relatively low. The presence of shrubs that birds can use as song perches to mark their territory may explain this preference. The positive associations found in this study between shrub cover and the presence of species in the warbler group and Song Sparrows tend to bear this out.

Waterfowl nesting

The various North American studies on the impact of livestock grazing on prairie habitat have shown that waterfowl nest density and nesting success are generally higher in locations where there is no disturbance caused by cattle (Higgins 1977). Hence, natural prairie that is not grazed or is subjected to light grazing pressure should support more nests and have a higher nesting success than pastureland. This situation cannot be attributed solely to trampling of nests by livestock; instead the major cause is degradation of the vegetation cover (Sayler 1962, Klett et al. 1988).

The results obtained in this study are fairly consistent with the findings reported for the western part of the continent. Clearly, the mean nest density observed (0.34 nests/ha) is fairly similar to that found on other islands along the St. Lawrence River (see Bélanger and Lehoux 1995), but well below the densities generally reported for lake islands in the Canadian Prairies (Giroux 1981, Duebbert 1982, Wills and Crawford 1989).

Conclusion

This study shows that grazing exceeding one cow/ha/year, is detrimental to the presence of birds that frequent the herbaceous spring flooded prairies of the islands along the St. Lawrence River, both quantitatively (number of individuals) and qualitatively (number of species). However, there is little overall difference between ungrazed and moderately grazed prairie. Certain species seem to prefer natural prairie, while others select moderately grazed ones. These findings have important implications for management, given that the mean nest density for ducks was also found to be positively associated with the vegetal cover obstruction measure, with little differences between moderately and ungrazed prairies. Thus, efforts aimed at improving the quality and composition of plant cover, such as delayed grazing, controlled burning (Fritzell 1975) or even short-term livestock grazing (Holechek et al. 1982), could serve to increase bird density in some prairie habitats. Furthermore, recent research by Barker et al. (1990) demonstrated that integration of wildlife and agriculture is possible on prairie subjected to livestock grazing. They noted that there were more duck nests in prairie habitat where specialized grazing systems had been implemented.

Consequently, with a view to pursue traditional farming activities along the St. Lawrence river and to preserving ground and shrub-nesting bird species (other than waterfowl) that frequent prairie habitats of the St. Lawrence River islands, electric fences or other structures, should be used to protect shrub zones and marsh shorelines with emergent plants. This would help to ensure the presence of the passerine species associated with older prairies and riparian habitats.

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Clipping effects on growth dynamics of Japanese brome

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Abstract

Japanese brome (*Bromus japonicus* Thunb.) has invaded many northern mixed prairie communities. Understanding how defoliation affects the life cycle of this species is critical for proper grazing management of communities infested with this annual. The objective of this study was to determine the effect of defoliation on growth of Japanese brome. Treatments included no clipping or clipping to 75- or 150-mm stubble height weekly or biweekly for 65 to 70 days in a greenhouse. Response of Japanese brome tiller numbers, leaf height, and above- and below-ground biomass were measured in 1991, 1992, and 1997. Clipping vegetative plants in 1991 reduced tiller numbers and leaf heights, whereas clipping plants with reproductive shoots in 1992 and 1997 increased tiller numbers and reduced leaf heights. Herbage accumulated during clipping, above-ground and total biomass were similar in 1991 and 1997, but lower in 1992. Accumulated herbage was reduced by reducing stubble height from 150 mm to 75 mm on a biweekly frequency and increasing the frequency of clipping from biweekly to weekly at either the 150-mm or 75-mm stubble height. Reducing the stubble height also reduced above-ground and total biomass. Increasing frequency of clipping did not generally affect total biomass. Some inflorescences were produced with even the most severe clipping treatment.

Key Words*: Bromus japonicus,* controlled environment, clipping intensity, clipping frequency

Resumen

"Japanese brome" (*Bromus japonicus* Thunb.) ha invadido muchas comunidades septentrionales de pradera mixta. El entender como la defoliación afecta el ciclo de vida de esta especie es crítico para llevar a cabo un manejo adecuado del apacentamiento de comunidades infestadas con esta especie anual. El objetivo de este estudio fue determinar el efecto de la defoliación en el crecimiento del "Japanese brome". El estudio se realizó en invernadero y los tratamientos evaluados fueron: no defoliación y defoliación a 75 mm y 150 mm de altura del rastrojo remanente con frecuencias de defoliación semanal y cada dos semanas. La respuesta del "Japanese brome" a la defoliación respecto al número de hijuelos, altura de la hoja y producción de biomasa áerea y subterránea fue medida durante 1991, 1992 y 1997. En 1991, la defoliación de plantas en estado vegetativo redujó el número de hijuelos y altura de la hoja, mientras que en 1992 y 1997 la defoliación de plantas con tallos reproductivos incrementó el número de hijuelos y redujó la altura de la hoja. El forraje acumulado durante la defoliación y la biomasa total y áerea fueron similares en 1991 y 1997, pero menores en 1992. En la frecuencia de defoliación de cada dos semanas, el forraje acumulado se redujó al reducir la altura del rastrojo remanente de 150 mm a 75 mm. El incrementar la frecuencia de defoliación de dos a una semana también disminuyó el forraje acumulado tanto en 150 mm como en 75 mm de altura del rastrojo remanente. Reducir la altura del rastrojo también redujó la biomasa áerea y total. El incrementar la frecuencia de defoliación generalmente no afectó la biomasa total. Algunas inflorecencias se produjeron aun con el tratamiento más severo de defoliación.

Invasion of Japanese brome (*Bromus japonicus* Thunb.), an introduced annual weedy grass, may negatively impact the forage base and grazers of many mixed prairie communities in the Northern Great Plains (Whisenant 1990, Haferkamp et al. 1993). Perpetuation of Japanese brome in these communities requires completion of its life cycle, beginning with seed germination and terminating with plant maturation and dissemination of viable seed. Reduction of Japanese brome will require interruption of this life cycle.

Reducing seed production by grazing or clipping is an effective method of interrupting the life cycle of annual plants, including bromes (Stewart and Hull 1949, Hulbert 1955, Laude 1957, Finnerty and Klingman 1962, Young and Tipton 1990). Grazing also can indirectly reduce annual brome biomass by reducing the amount of mulch on the soil surface. The mulch benefits germination and seedling establishment of Japanese brome (Whisenant 1990) and downy brome (*Bromus tectorum* L.) (Evans and Young 1970). Pfeifer (1985) found clipping Japanese brome to a 50-mm stubble height in the

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field reduced subsequent plant height growth and above-ground biomass, while tiller density increased. These results differ from her greenhouse studies wherein clipping increased above-ground biomass, but did not affect tiller density. Competitive interactions with annual bromes vary also by species and season (Tausch et al. 1990). Grazing at different times of the year may shift the competitive balance between annual bromes and other species in the community.

Studies are lacking that quantify the effect of intensity and frequency of clipping on above- and below-ground biomass of Japanese brome. The objective of this greenhouse study was to determine the response of Japanese brome, as measured by tiller number, leaf height, and above- and below-ground biomass, to varying intensities and frequencies of clipping.

Materials and Methods

Japanese brome seedlings were grown in 30 greenhouse boxes (inside dimensions of 10.2 cm wide, 32.8 cm long, and 73.7 cm deep) in 1991 and 1992 (Haferkamp and Currie 1973) and 45 PVC tubes (80 cm tall and 20 cm diameter) in 1997. Each container was uniformly packed with soil (Typic Ustochrepts, fine-silty, mixed, frigid). Seedlings were grown from seed collected on the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. (Haferkamp et al. 1994b). Seeds were germinated on paper towels in the bottom of aluminum trays in a germinator with controlled environment of alternating 12-hour periods of 8 and 23° C with light supplied by cool-white fluorescent bulbs (PAR = 30 umoles m^{-2} sec^{-1}) during each 12-hour 23°C period (Haferkamp et al. 1994a). Soil was added to each tray when seedlings were about 10 mm tall, and trays were moved into the greenhouse. When emerging seedlings were about 25 mm tall, several were transplanted in late winter into each container. When fully established, populations were hand-thinned to 2 healthy seedlings per container. Plants were watered to maintain active growth during the study. Natural light regimes were used, except that illumination from an exterior night light was evident within the greenhouse in 1991. This light was removed before beginning the 1992 and 1997 studies. Air temperatures were maintained near 10°C in the winter and below 38°C during spring and summer.

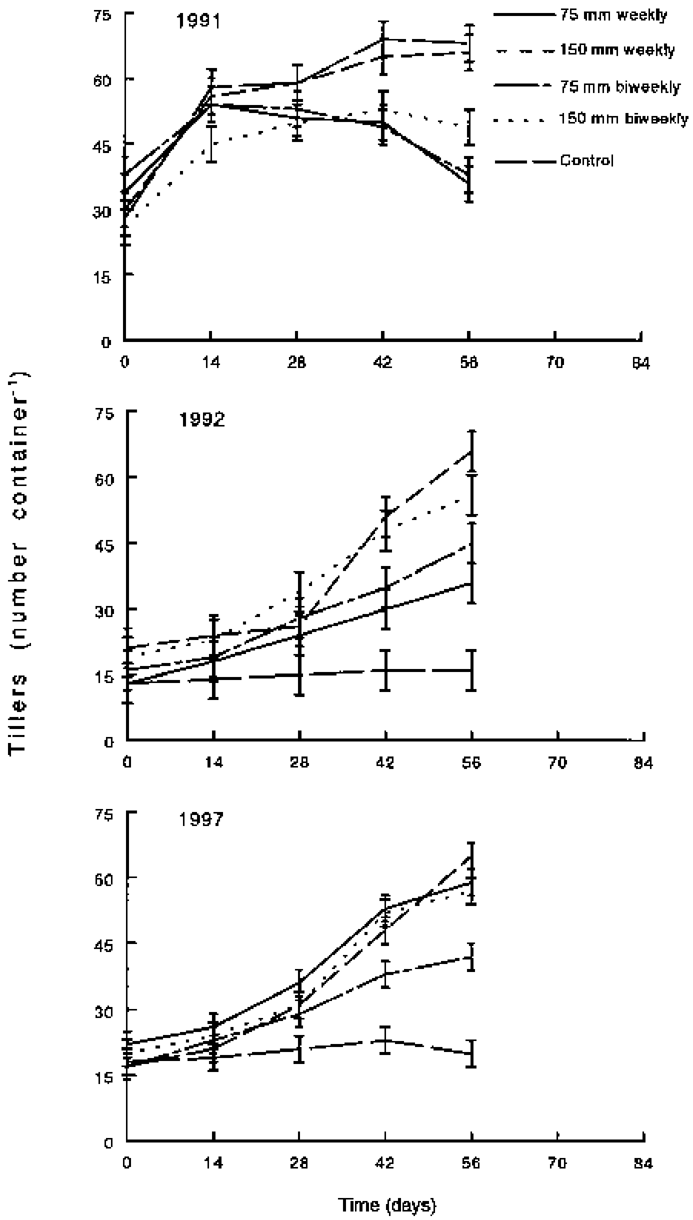

Fig. 1. Least square means of tiller counts ± standard errors for a significant 3-way interaction of year by treatment by date for Japanese brome plants.

Clipping treatments were applied during a 65- to 70-day period from 20 June to 30 August 1991, 4 May to 8 July 1992, and 1 May to 8 July 1997. We measured leaf heights, from the soil surface to the tip of the longest leaf, and counted tiller numbers weekly before and after clipping treatments began. Due to variation in duration of clipping and final harvest periods, we chose day 52 as the final date for leaf height measurements and tiller counts and day 84 as the final harvest date. Five treatments included an unclipped control and plants clipped to either a 75- or 150-mm stubble height either weekly or biweekly. When clipping treatments began, leaf heights averaged 30 cm in both 1991 and 1992 and 38 cm in 1997. Tiller numbers averaged 32 per container in 1991, 16 in 1992, and 19 in 1997. Inflorescences emerged soon after treatment periods began in both 1992 and 1997. Sixty-six percent of the plants produced inflorescences 14 days after clipping began in 1992, whereas 80% produced inflorescences 14 days after clipping was initiated in 1997. More than 90% of the plants had exerted inflorescences on each measurement date after day 14 during these 2 studies.

As plants were processed at the end of each study (assigned day 84 in figures), herbage was clipped to the designated stubble height of 75 or 150 mm for the 2 clipping treatments or at the soil surface for control plants. The stubble remaining from the 75- and 150-mm treatments was clipped at the soil surface. Roots and crowns were washed from the soil over a 6-mm screen, and roots were clipped from crowns. All plant material including herbage accumulated during weekly or biweekly clippings and above- and below-ground biomass collected at the end of each study were dried for 48 hours at 60°C and then weighed.

Treatments were factorially arranged in a randomized complete-block design with 6 blocks in 1991 and 1992 and 9 blocks in 1997. Before treatments began, plants were rearranged within the greenhouse to provide uniform plant size within each block. Analysis of variance was used to test the effect of clipping intensities (stubble height) and frequencies on total root, shoot, and crown biomass and herbage accumulated during clipping by date of harvest. A repeated measures analysis of variance was used to test the effect of clipping intensities or frequencies on tiller counts and maximum leaf heights. Main effects of year and treatment and their interaction were tested with the residual variation blocks within year and treatment; effects of date and interactions of date with year and treatment were tested with residual intrablock variation. The Least Significant Difference (LSD) method ($P \leq 0.05$) protected by a prior F-test ($P \leq 0.05$) was used for comparing means. All differences discussed are significant at the $P \leq 0.05$ level unless otherwise noted.

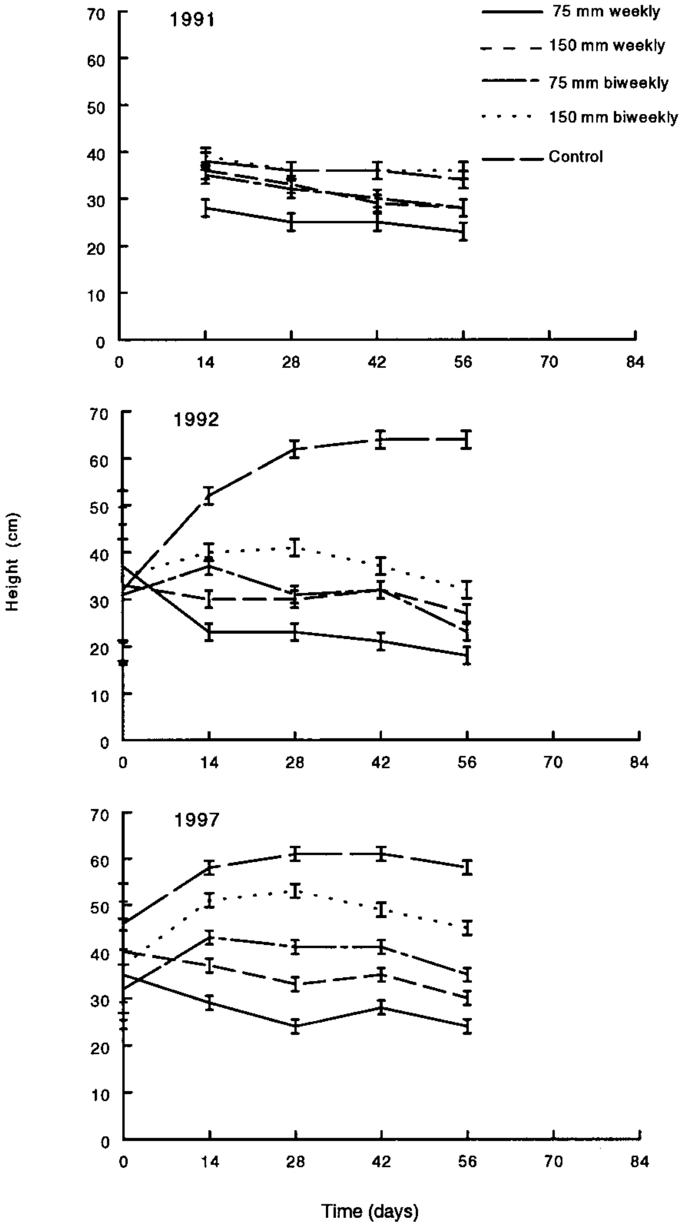

Fig. 2. Least square means of leaf heights ± standard errors for a significant 3-way interaction of year by treatment by date for Japanese brome plants. Leaf heights were not measured until day 7 in 1991.

Results

Tiller Numbers

Treatment differences in tiller numbers were not obvious until 42 days after clipping began each year (Fig. 1). On days 42 and 56, maximum numbers were produced by unclipped controls and plants clipped to 150 mm weekly in 1991; plants clipped to 150 mm weekly and biweekly in 1992; and plants clipped to 75 and 150 mm weekly and 150 mm biweekly in 1997. Within treatments, tiller numbers increased by day 14 and remained relatively constant or in some cases decreased in 1991, whereas in 1992 and 1997, tiller numbers increased during the study period for all treatments except unclipped controls.

Leaf Heights

Clipping significantly affected leaf heights by 14 days after treatments began each year. Greater leaf heights on unclipped controls in 1992 and 1997 compared to 1991 reflect the internode elongation of reproductive shoots produced in both 1992 and 1997. Maximum leaf heights were maintained on the unclipped controls and plants clipped to 150 mm biweekly in 1991, and unclipped controls in 1992 and 1997 (Fig. 2). Leaf heights tended to decrease over time in 1991 for plants clipped weekly to 75 and 150 mm and those clipped biweekly to 75 mm. Heights decreased significantly over time for all clipped plants in 1992 and 1997.

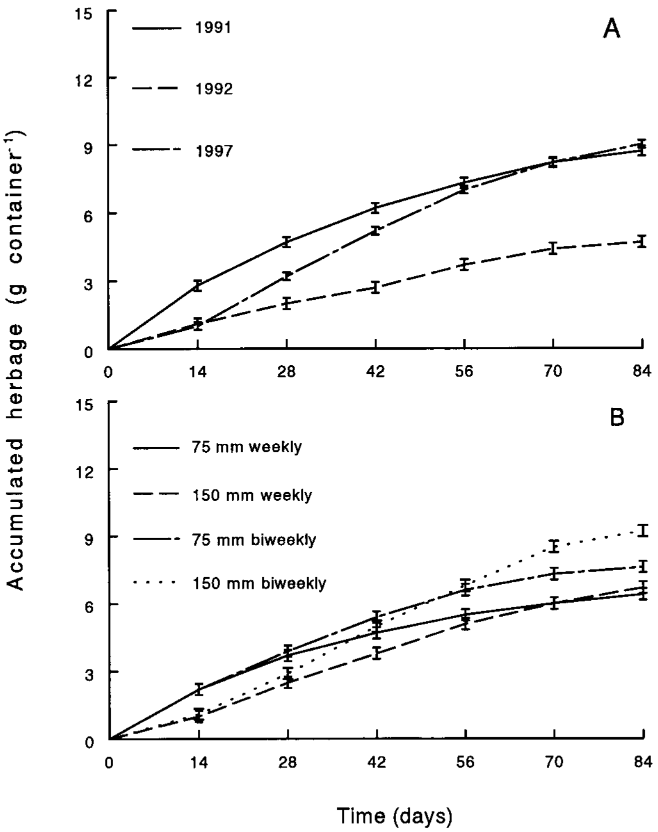

Fig. 3. Least square means for accumulated herbage ± standard errors for significant 2-way interactions of year by date (A) and treatment by date (B) for Japanese brome plants.

Heights of unclipped control plants remained stable in 1991 and 1997 but increased toward the end of the sampling period in 1992.

Accumulated Clipped Herbage

Accumulated herbage was greater in 1991 than in 1992 or 1997 for the first 42 days (Fig. 3A). Thereafter, accumulated herbage was greatest in 1991 and 1997 and least in 1992. Herbage accumulation was greater for the first 28 days when plants were clipped at the 75-mm stubble height (Fig. 3B). However, by day 56 more herbage was accumulated by clipping biweekly to 150 mm than clipping weekly to 75 mm. Maximum herbage was accumulated from plants clipped biweekly to 150 mm. More herbage was accumulated from plants clipped biweekly to 75 mm than from plants clipped weekly to 75 or 150 mm.

Above- and Below-ground Biomass

Total and above-ground biomass yields were greater in 1991 and 1997 than in 1992 (Fig. 4A). Total and above-ground biomass were greatest for unclipped control plants, intermediate for plants clipped to 150 mm, and least for plants clipped to 75 mm (Fig. 4B). Below-ground biomass varied significantly among years within treatments (Table 1). Biomass production was similar among years for most clipping treatments, but was greater in 1997 than 1992 for plants clipped biweekly to 150 mm and greater in 1991 than in 1992 or 1997 for unclipped controls. Below-ground biomass was greater for unclipped controls than all other treatments in 1991; similar among clipping treatments in 1992; and greater for plants clipped biweekly to 150 mm than for control plants or those clipped weekly or biweekly to 75 mm in 1997. Frequency of clipping did not significantly affect above-ground ($P = 0.057$), below-ground ($P = 0.910$), or total ($P = 0.111$) biomass.

Table 1. Below-ground biomass produced by Japanese brome plants treated with 1 of 5 clipping treatments during 3 years.

Year	weekly 75mm	weekly 150mm	biweekly 75mm	biweekly 150mm	control
			(g container^{-1})		
1991	${}_{a}2.5^{C}$	${}_{a}6.2^{B}$	${}_{a}4.0^{BC}$	${}_{ab}5.1^{BC}$	${}_{a}10.0^{A}$
1992	${}_{a}1.2^{A}$	${}_{a}3.6^{A}$	${}_{a}1.2^{A}$	${}_{b}2.3^{A}$	${}_{b}3.1^{A}$
1997	${}_{a}3.1^{C}$	${}_{a}5.9^{AB}$	${}_{a}3.7^{BC}$	${}_{a}6.6^{A}$	${}_{b}3.6^{BC}$

Means within a year followed by the same upper case superscript or within a treatment preceded by the same lower case subscript are not significantly ($P \geq 0.05$) different.

Discussion

Reproductive Status

Baskin and Baskin (1981) suggested vernalization was not an absolute requirement for Japanese brome to flower as reported by Hulbert (1955); rather they found exposure to short days prior to exposure to long days stimulated flowering. This study supports Baskin and Baskin (1981) in that our plants did not flower in 1991 when exposed to the almost continuous light provided by natural day light and an exterior night light.

Morphological Status

Observed responses for tiller number and leaf height in 1991 are characteristic of plants producing culmless vegetative shoots with apical meristems maintained near the soil surface while grown in a fertile well-watered environment. Hyder (1974) reported culmless vegetative shoots are well adapted to frequent mowing and grazing. He reported leaf growth stops during unfavorable conditions, but cell division and expansion resume in both apical and intercalary meristems upon the resumption of favorable conditions (e.g., temperature and soil water). Culmless vegetative shoots remain active in producing leaf

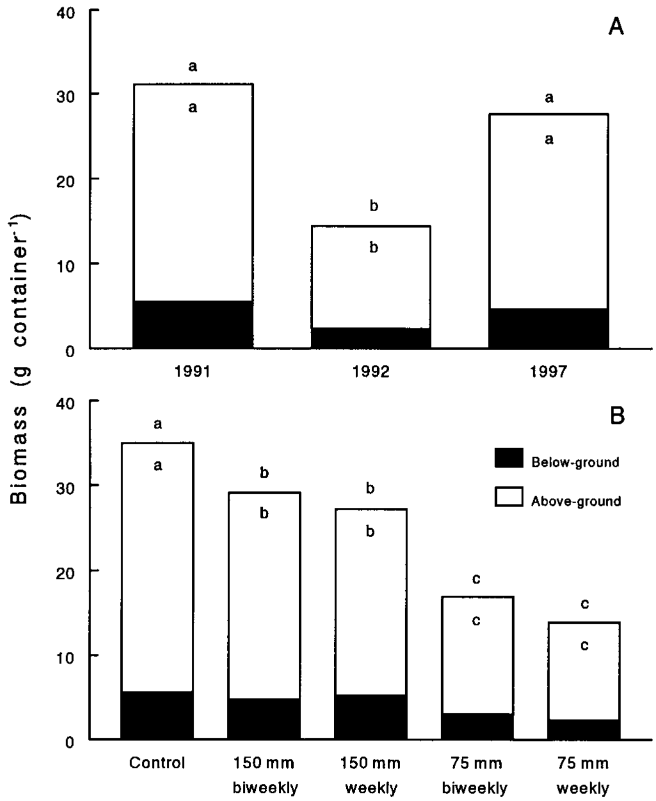

Fig. 4. Least Square Means for above- and below-ground biomass for significant main effects of year (A) and treatment (B). Similar lower case letters above total biomass and within aboveground biomass denote lack of significance (P≥0.05) between years or treatments.

tissue unless the shoot apex becomes reproductive or death occurs. Plants studied in 1992 and 1997 responded as plants initially with culmless vegetative shoots that eventually differentiated into culmed reproductive shoots. Few tillers were produced by unclipped plants, but once reproductive shoots were clipped, plants tillered rapidly within the greenhouse environment.

The reduction in below-ground biomass with all clipping treatments in 1991 was probably the result of removing actively photosynthesizing leaves. Tiller density was high for all plants when clipping began on actively growing vegetative tillers. Removal of leaf material, thus, probably reduced the amount of carbohydrate available for root growth. In contrast, clipping increased tiller numbers in 1992 and 1997. Findings in 1997 suggest below-ground biomass increased most with the least intensive and frequent clipping schemes that allowed the greatest accumulation of leaf area. Lack of differences among below-ground biomass values in 1992, as well as reduced above-ground biomass production, suggest plants may have suffered environmental stress from high temperature, lack of soil water, or insects. Reduced leaf area would have impacted the response of below-ground biomass to clipping regimes.

Management Implications

These findings relate to situations where soil water is adequate for regrowth of Japanese brome plants after defoliation. The environmental conditions near Miles City (Fig. 5) would allow regrowth during spring in many years. Care must be exercised in extrapolating from greenhouse findings to field environments. Briske and Richards (1995) suggest environmental variables which promote growth, (e.g., favorable temperature, irradiance, water and nutrient availability), generally promote tillering as well. Pfeifer (1985) found Japanese brome plants stopped growing as the growing season advanced in Kansas due to reduced soil water availability and high temperatures. Whole plot shading reduced the heat load and allowed plants to keep growing. In contrast, unshaded plants produced the most tillers during the duration of the greenhouse study where water and temperatures were controlled for optimum growth. She also found clipping intervals of 2, 3, or 4 weeks best for regrowth of Japanese brome in the field, but regrowth was similar among all intervals in the greenhouse. Difference in above-ground biomass between unclipped and clipped plants reportedly resulted from differences in number of tillers and not weight of tillers. The lack of a consistent tillering response often found between different years or controlled environments and the field is due to the apparent complexity of the physiological mechanisms regulating axillary bud growth (e.g., apical dominance) and the large number of potentially intervening factors, (e.g., environmental variables, species specific responses, stage of phenological development, and frequency and intensity of defoliation) (Briske and Richards 1995).

The 1991 findings relate to situations where Japanese brome seeds were disseminated on spring dates too late for optimum vernalization and photoperiod response. Baskin and Baskin (1981) proposed a scenario where Japanese brome seed remains on dead erect plants until spring when habitat temperatures are too high for induction of secondary seed dormancy or vernalization. Non dormant seed would germinate if soil water was sufficient, but the resulting plants would not flower until the following spring after they received vernalization and the transition from short days to long days during winter and spring. Baskin and Baskin (1981), however, found only a few newly germinated seeds in the spring. Similarly, Karl (unpublished data) found only a few seedlings emerging in the spring on our study locations.

Heavy grazing or intensive clipping, as reported in this and other studies, reduces above- and below-ground biomass and seed production. Thus seedling density is reduced with a reduction in the amount of seed, as well as, mulch or litter. A dense litter cover reduces evaporation of soil water and thus provides an optimum environment for germination and seedling emergence. Vallentine and Stevens (1994) and Mosley (1996) sug-

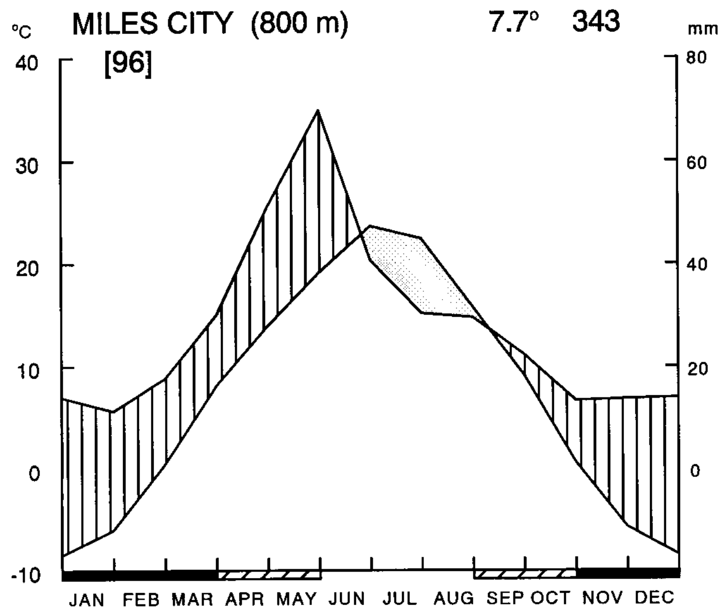

Fig. 5. Climate diagram for Miles City, Mont. Mean monthly precipitation (mm) and temperature (°C) for 96-year period indicate mesic spring, early summer, and fall periods interrupted by late summer and early fall drought (stippling). Winter precipitation occurs as snow. Months shaded in black have average minimum temperatures <0°C. Those with diagonal lines have absolute minimum temperatures <0°C. Figure follows standard form of Walter (1985).

gest there is a rather narrow early spring window when grazing can suppress downy brome growth, seed production, and mulch buildup. This approach would require high-density grazing for a short duration, during which time downy brome would be closely defoliated and/or seed production prevented. Precisely timing grazing to reduce selection of perennial grasses or allowing them adequate time to recover from defoliation before the end of the growing season is challenging.

Defoliation early in the growing season is critical for controlling annual bromes. Hulbert (1955) found downy brome was difficult to eliminate by mowing at the purple stage. Seeds were already sufficiently developed to germinate at a later date. Haferkamp et al. (1996) also found Japanese brome seed germinates in June when it is still green. Finnerty and Klingman (1962) found mowing about 1 week after inflorescences emerged was the most appropriate time to control downy brome. Even this treatment did not eliminate downy brome plants from plots; a few young tillers always emerged from mowed plants. Defoliation does not always reduce annual brome production. Ganskopp and Bedell (1979) found grazed downy brome plants produced more forage than ungrazed plants when soil water was available for regrowth.

The tillering response reported for downy brome by Finnerty and Klingman (1962) could occur with grazed or mowed Japanese brome plants in the Northern Great Plains. Terminating grazing or mowing when soil water is available for regrowth of associated perennial grasses may also prove advantageous for annual bromes. It is unlikely all plants and tillers will be grazed. Thus, there will always be some annual brome plants producing viable seed to replenish the seed bank. Whisenant (1990) suggests greater reduction of annual bromes can be expected when precipitation is below normal following the year of burning or in our case clipping or grazing. This phenomena is a result of reduction in litter accumulation, which will reduce annual brome recruitment, seed production, and seed banks. As water becomes limiting, litter becomes more important in population dynamics. As suggested by Vallentine and Stevens (1994), sufficient information probably does not presently exist for developing the precise grazing plan needed for exerting biological control, but further research seems warranted.

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Response of white-tailed deer foods to discing in a semiarid habitat

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Abstract

Discing strips of rangeland to increase wildlife foods is a common management practice. I tested the hypotheses (1) annual discing results in greater canopy cover of annual forbs preferred by white-tailed deer (*Odocoileus virginianus* Raf.) than discing at less frequent intervals of time, (2) frequent discing reduces the abundance of preferred perennial forbs, and (3) discing only once results in greater total canopy cover of annual and perennial forbs preferred by deer. The experimental design was a split-plot with soil series (Ramadero loam or Delfina fine sandy loam) as main plots and discing treatment in October as subplots. Discing treatments were (1) no treatment (control); (2) discing once in 1990; (3) discing once in 1994; (4) discing in 1990 and 1994; (5) discing in 1990, 1992, and 1994; and (6) discing annually from 1990–1994. Discing increased canopy cover of annuals preferred by white-tailed deer and increased canopy cover of unpalatable forbs, but decreased preferred perennials. Canopy cover of forbs eaten, but not preferred by deer, increased following discing. Based on these results, soil disturbance by discing is not recommended as a habitat improvement practice in the semiarid western Rio Grande Plains of Texas if the objective of management is to increase canopy cover of forbs preferred by white-tailed deer.

Key Words: forbs, habitat improvement, *Odocoileus virginianus* Raf., patches, plant succession, semi-arid environments

Resumen

El rastreo de franjas de pastizal para incrementar los alimentos de la fauna silvestre es una práctica común de manejo. Probé las siguientes hipótesis 1) el rastreo anual resulta en una mayor cobertura de la copa de las hierbas anuales preferidas por el venado cola blanca (*Odocoileus virginianus*. Raf.) que rasterando a intervalos menos frecuentes, 2) el rastreo frecuente reduce la abundancia de hierbas perennes preferidas y 3) rastreando solo una vez resulta en una cobertura total mayor de hierbas anuales y perenes preferidas por el venado. El diseño experimental fue el de parcelas divididas, la parcela principal fue series de suelo (Ramadero y Delfina) y la subparcela fue el tratamiento de rastreo en Octubre. Los tratamientos de rastreo fueron: (1) no rastreo (control); (2) rastreo una sola vez en 1990; (3) rastreo una sola vez en 1994; (4) rastreo en 1990 y 1994; (5) rastreo en 1990, 1992 y 1994 y (6) rastreo anual de 1990 a 1994. El rastreo incrementó la cobertura de la copa de las especies anuales preferidas por el venado cola blanca e incrementó la cobertura de copa de hierbas no preferidas pero también redujó las especies perennes preferidas. La cobertura de la copa de las hierbas consumidas pero no preferidas por el venado cola blanca se incrementó después del rastreo. Basado en estos resultados se puede concluir que si el objetivo es incrementar la cobertura de las hierbas preferidas por el venado cola blanca, el disturbio del suelo por el rastreo no es recomendado como una práctica de mejoramiento del hábitat en las regiones semiáridas del oeste de las planicies del Río Grande.

Discing strips of rangeland is commonly recommended by wildlife specialists as a management tool to increase the abundance of early-successional annual forbs preferred by white-tailed deer (*Odocoileus viginianus* Raf.) and to provide herbage and seeds for northern bobwhites (*Colinus virginianus* Merr.) (Arnold and Drawe 1979, Webb and Guthery 1983, Nurdin and Fulbright 1988). In Florida, discing promoted a variety of valuable food plants for northern bobwhites (Landers and Mueller 1986:21-23). Discing in northwest Texas promoted several plant species important for wildlife, but forb production and density on the disced strips were relatively low (Webb and Guthery 1983). Discing sites dominated by whitebrush [*Aloysia gratissima* (Gill. & Hook.) Trancoso] did not consistently increase forbs eaten by white-tailed deer in the western Rio Grande Plains of Texas (Bozzo et al. 1992).

There is little information in the literature regarding the frequency of discing needed to maintain increased abundance of wildlife food plants. Jones et al. (1993) compared discing once with discing 2 years in a row and reported that discing 2 years in a row resulted in greater canopy cover of northern bobwhite food plants in the South Carolina Piedmont. In the Coastal Plain of South Carolina, neither treatment increased

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abundance of northern bobwhite food plants.

Frequent, intense disturbances result in patches being occupied only by quickly maturing annuals, whereas infrequent disturbances allow establishment of slower-growing perennials (Connell 1978). Perennial forb species are more important in white-tailed deer diets than annuals (Scifres 1980). Frequent discing is a desirable habitat management practice for white-tailed deer if the practice consistently results in increased abundance of perennial and annual forbs preferred by deer. Conversely, frequent discing is undesirable if the practice reduces preferred perennial forbs.

My objective was to determine the frequency of discing that produces the greatest canopy cover of herbaceous plants preferred by white-tailed deer. I tested the hypotheses that (1) annual discing results in greater canopy cover of annual forbs preferred by white-tailed deer than discing at less frequent intervals of time; (2) frequent discing reduces the abundance of perennial forbs preferred by deer; and (3) discing only once allows reestablishment of perennial forbs, resulting in greater total canopy cover of annual and perennial forbs preferred by deer than annual discing or no discing.

Materials and Methods

Study Area

Research was conducted on the El Tecomate Ranch (98°50' longitude, 26°45' latitude) in Starr County, Tex., 40 km north of Rio Grande City. Dominant vegetation on the study area was a honey mesquite (*Prosopis glandulosa* Torr.)-mixed brush community (Thompson et al. 1972). Average annual rainfall was 43.9 cm (1931–1962). The average annual maximum temperature was 30.6°C and the average annual minimum was 16.3°C. Soils on study sites were Ramadero loam or Delmita fine sandy loam. Rainfall within the study area was monitored with an electronic rain gauge.

The 809-ha study area was not grazed by livestock during 1990, 1991, and in 1995. Cattle stocking rates (steers) were 8.4, 19.3, and 17.8 ha/animal unit during 1992, 1993, and 1994, respectively. Cattle grazed from late-April to mid-August, late April to October, and July to August during 1992, 1993, and 1994, respectively. An average of 9 ± 0.4 deer/km ($\bar{x}$ ± SE, n = 9) were counted during fall and winter from a helicopter during 1990–1995. DeYoung (1985) found that 33 to 67% of the deer actually present are counted during helicopter counts in south Texas.

Grazing by cattle and white-tailed deer possibly differentially affected herbaceous plant species composition among discing treatments. Study plots were not fenced to exclude herbivores and grazing effects were not documented. Effects of cattle grazing on treatments were minimized because (1) cattle were not present during 1990, 1991, and 1995; (2) cattle were grazed for only 2–6 months during 1992-94; (3) cattle numbers were low relative to the stocking rates normally used in the area; and (4) cattle were removed in August, except during 1993. Summers are generally dry in Starr County, whereas the highest rainfall months are September and October. Thus, the study sites were free of cattle during the highest rainfall period and for 6 months thereafter.

Table 1. Scientific and common names of herbaceous plants encountered on control and disced plots during 1991–1995, Starr County, Texas, in 3 categories based on data from Everitt and Drawe (1974), Arnold and Drawe (1979), and Hehman (1995).

Plant category and scientific name	Common name	Season of Growth
Preferred Annuals		
Aphanostephus ramosissimus DC.	Plains lazydaisy	Warm
Aphanostephus skirrhobasis (DC.) Trel.	Kidder lazydaisy	Warm
Euohorbia prostata Ait.	Prostrate euphorb	Warm
Gaura brachycarpa Small	Plains gaura	Cool
Preferred Perennials		
Acleisanthes obtusa (Choisy) Standl.	Berlandier trumpets	Warm
Ambrosia cumanensis Kunth in H.B.K.	Western ragweed	Warm
Commelina erecta L.	Narrowleaf dayflower	Warm
Cynanchum barbigerum (Scheele) Shinners	Bearded swallow-wort	Warm
Lantana macropoda Torr.	Veinyleaf lantana	Warm
Menodora heterophylla Moric.	Low menodora	Warm
Parthenium confertum Gray	Lyreleaf parthenium	Warm
Physalis cinerascens (Dun.) A. S. Hitchc.	Beach groundcherry	Warm
Ratibida columnifera (Nutt.) Woot. & Standl.	Upright prairie cone flower	Warm
Solanum triquetrum Cav.	Texas nightshade	Warm
Trixis inula Cranz.	Mexican trixis	Cool
Wedelia hispida H.B.K.	Orange zexmenia	Warm
Xanthisma texanum DC.	Sleepy daisy	Warm
Unpalatable species		
Palafoxia texana DC.	Texas palafoxia	Warm
Salsola iberica Senn. & Pau	Russian thistle	Warm
Verbesina enceliodes (Cay.) Benth. & Hook. ex Gray	Cowpen daisy	Warm

Experimental Design and Vegetation Sampling

Six, 10-m X 40-m plots separated by 10-m-wide buffers were delineated within each of 4 blocks on Ramadero loam and 4 blocks on Delmita fine sandy loam. Six treatments were randomly assigned to the plots within each of the 4 blocks within each soil series. Blocks within a soil series were within 0.5 km of each other and soil series were <1 km apart. Treatments were (1) no treatment (control); (2) discing once in 1990; (3) discing once in 1994; (4) discing in 1990 and 1994; (5) discing in 1990, 1992, and 1994; and (6) discing annually during 1990–1994. Discing was conducted each October during 1990-1994. I selected October based on results of unpublished data that indicated a greater response of forbs to fall discing than to spring or summer discing. Treatment plots were disced with a heavy disc with 2 gangs of 107-cm-diameter blades. The disc was pulled by a crawler tractor (Caterpillar D-7) and 2 passes were made within each plot on each treatment date. Mean depth of disc penetration in Ramadero loams ranged from 14 ± 0.8 (n = 4) cm in 1993 to 19 ± 0.3 cm in 1994. In Delmita fine sandy loams, mean depth of disc penetration ranged from 12 ± 0.2 cm in 1990 to 18 ± 0.5 cm in 1994.

Canopy cover and frequency of herbaceous species were ocularly estimated during March 1991–1995 within twenty-five, 20 X 50-cm quadrats placed in a restricted-random fashion within each soil series, treatment, and replication combination. Sampling was conducted during March because I observed that the peak abundance of cool-season forbs in the study area generally occurs in March. Herbaceous plant species were categorized as "preferred annuals", "preferred perennials", "preferred annuals and perennials", "unpalatable" species (Table 1), and "other" species. Preferred annual and perennial species were those ranked in the top 40 species found in deer diets <25 km from El Tecomate Ranch by Arnold and Drawe (1979). "Other" species were those not ranked in the top 40 species found in deer diets but recorded as present in deer diets on El Tecomate Ranch (Hehman 1995) and <25 km from El Tecomate Ranch by Everitt and Drawe (1974) and Arnold and Drawe (1979). "Unpalatable" species were not encountered in deer diets on El Tecomate Ranch (Hehman 1995) or <25 km from El Tecomate Ranch by Arnold and Drawe (1979).

Statistical Analyses

I used analysis of variance (PROC GLM; SAS Inst. Inc. 1988) for a split-plot experimental design with soil series as main plots and discing treatment as subplots to test for significant ($P < 0.05$) soil series and discing treatment main effects and interactions. The timing of discing, with certain plots disced once and others at periodic intervals of time, resulted in different treatment combinations in different years. Two treatments, control and disced once in 1990, were compared in 1991; 3 treatments (control, disced once in 1990, and annual discing) were compared in 1992; 4 treatments (control, disced once in 1990, disced in 1990 and 1992, and annual discing) were compared in 1993 and 1994; and 6 treatments (control; disced once in 1990, disced once in 1994, disced in 1990 and 1994; disced in 1990, 1992, and 1994; and annual discing) were compared in 1995. PROC GLM was used because sample sizes were unequal. In March 1991 there were 8 control plots (2 soil series x 4 blocks) and 32 plots disced in October 1990 (2 soil series x 4 blocks x 4 plots); in March 1992 there were 8 control plots, 8 plots disced in October 1990 and 1991 (2 soil series x 4 blocks), and 24 plots disced in October 1990 (2 soil series x 4 blocks x 3 plots). Separate analyses were conducted for each year of sampling and for each preference class (preferred annual forbs, preferred perennial forbs, preferred annuals and perennials combined, other herbaceous plant species, and unpalatable forbs) except for 1993 and 1994. In analyses, arcsin transformed canopy cover (%) was the dependent variable. When the soil series X discing treatment interaction was significant ($P \leq 0.05$), I conducted a separate analysis of variance for a randomized, complete-block design for each soil series with arcsin transformed canopy cover (%) as the dependent variable and discing treatment as the independent variable to allow means separation. I used the Tukey-Kramer option in SAS for comparing the least squares means ($P \leq 0.05$) for arcsin transformed percent canopy cover.

Repeated measures analyses were conducted for 1993 and 1994 data with year as the repeated measure since sample sizes among treatments were equal between sampling dates (Cody and Smith 1991). When the discing treatment X sampling date interaction was significant ($P \leq 0.05$), I conducted a separate analysis of variance for each sampling date (1993 or 1994) as previously described.

Certain plant species colonize large patches more readily than smaller patches (Glenn and Collins 1992, Arnthórsdóttir 1994). However, there is little reason to expect that our results would differ among patch sizes normally created in rangeland discing. Glenn and Collins (1992) compared colonization on regional versus local scales, whereas patches compared by Arnthórsdóttir (1994) were ≤200 cm^2.

Results

Discing during October generally increased ($P \leq 0.05$) canopy cover of preferred annuals the following March compared to controls (Table 2). Exceptions occurred in March 1992 when canopy cover on disced plots and controls did not differ significantly ($P > 0.05$). Also, the soil series X discing treatment interaction was significant ($P = 0.001$) in March 1995. No preferred annuals were present on disced treatments or controls on Ramadero loam soils. Canopy cover of preferred annuals on Delfina fine sandy loams ranged from 1±1 to 3±1% ($\bar{x}$ ±SE) compared to <1±<1% on controls. On Delfina fine sandy loam soils in March 1995, canopy cover of annuals was greater ($P \leq 0.05$) on disced plots than controls, but no significant ($P \leq 0.05$) differences in canopy cover of annuals existed among the discing treatments themselves.

Canopy cover of preferred perennials was generally greater ($P < 0.05$) on controls than on disced plots. The soil series X discing treatment interaction was significant ($P = 0.007$) in March 1993–1994 for preferred perennial canopy cover. Preferred perennials were virtually absent from Ramadero soils during March 1993–1994, with canopy cover ranging from <1±<1% on annually disced plots to 1±<1% on controls and not differing significantly ($P > 0.05$) among treatments. Control plots sup-

Table 2. Mean canopy cover (%) of herbaceous plants during March 1991–1995 on Delfina fine sandy loam and Ramadero loam in plots not disced (control) or disced during October 1990; 1994; 1992 and 1994; 1990, 1992, and 1994; or 1990–1994; Starr County, Tex.

Treatment	n	Preferred annuals $\bar{x}$	SE	Preferred perennials $\bar{x}$	SE	Preferred annuals and perennials $\bar{x}$	SE	Other species eaten by deer $\bar{x}$	SE	Unpalatable species $\bar{x}$	SE
		- - - - - - - - - -	- - - -	- - - - -	- - - (%)	- - - -	- - - - -	- - - - -	- - - -	- - - - -	
						1991					
Control	8	2b[1,2]	I	4a	1	6b[2]	1	21b	4	<lb	<1
Disc-90	32	13a	1	lb	<I	14a	1	45a	3	3a	1
						1992					
Control	8	14a[2]	4	11a	4	25a[2]	5	80b	9	1c	<1
Disc-90	24	23a	3	4b	I	26a	3	106a	3	l0b	2
Annual	8	21a	4	lb	<1	22a	4	96ab	8	24a	7
						1993 and 1994					
Control	16	2b	1	3[3]	1	6[4]	2	15b[2]	3	0c	
Disc-90	32	7a	2	2	<1	9	2	29a	3	4b	1
Disc-90,92	16	7a	2	1	<1	8	2	25a	3	l0b	2
Annual	16	5a	2	<1	<1	5	2	20ab	2	21a	3
						1995					
Control	8	<1[3]	<1	5a[2]	1	5a[2]	1	23a	4	<1c	<1
Disc-90	8	1	<1	2b	1	3b	1	38a	8	2c	1
Disc-94	8	1	<1	<1c	<1	lb	<1	13b	2	<1c	<1
Disc-90,94	8	1	1	0bc		lb	1	19a	2	5bc	3
Disc-90,92,94	8	1	1	<lbc	<1	lb	1	20a	5	l3ab	6
Annual	8	1	<1	<lbc	<1	lb	<I	19a	4	21a	7

[1]Means followed by the same letter are not significantly (P> 0.05) different based on Tukey's HSD. Analyses were for arcsin transformed means; means reported in the table are not transformed.
[2]Significant (P<0.05) difference between soil series
[3]Significant (P<0.05) soil series x treatment interaction.
[4]Significant (P<0.05) treatment x sampling date interaction.

ported greater (P≤0.05) canopy cover (6±2%) of preferred perennials on Delfina fine sandy loams than plots disced annually and plots disced in October 1990 and 1992 (1±<1%).

On all disced treatments, canopy cover of annual and perennial preferred species combined was lower (P<0.05) than controls or did not differ significantly (P > 0.05) from controls except in March 1991 and 1993. Canopy cover on disced plots exceeded (P<0.05) controls in March 1991. There was a significant (P = 0.020) sampling date x discing treatment interaction for annual and perennial preferred species combined in March 1993 and 1994. In March 1993, canopy cover of preferred annuals and perennials combined was greater (P≤ 0.05) on plots disced in 1990 (15±2%) than on controls (7±2%). Canopy cover did not differ significantly (P>0.05) from controls on plots disced in 1990 and 1992 (12±4%) and annually disced plots (9±2%). In March 1994, canopy cover of annual and perennial preferred species combined was lower (P≤0.05) on annually disced plots (1±1%) than on controls or plots disced in 1990 (3±1%) or plots disced in 1990 and 1992 (4±1%).

With the exception of annually disced plots, herbaceous species eaten by deer but not preferred ("other species") had greater (P>0.05) canopy cover on discing treatments than on controls during March 1991–1994 (Table 2). Canopy cover of unpalatable plants was greater (P>0.05) on disced plots than on control plots, except in 1995 when canopy cover of unpalatable plants did not differ significantly (P>0.05) on plots disced one time only in October 1990 or October 1994. Annually disced plots contained the greatest (P<0.05) canopy cover of unpalatable plants.

Discussion and Conclusions

Production of herbaceous plants in semiarid environments is strongly governed by rainfall. Consequently, results of discing may be inconsistent from year to year because of variation in rainfall. For example, in this study, during March 1994 low rainfall (Fig. 1) may have inhibited disced plots from producing sufficient canopy cover of herbaceous plant species to detect differences among treatments.

I rejected the hypothesis that annual discing results in greater canopy cover of annual forbs preferred by deer than discing at less frequent intervals. Annual discing did not increase preferred annual forbs compared to plots disced only once, but consistently increased unpalatable forbs. Based on these results, annual discing is an undesirable management practice for increasing forbs eaten by white-tailed deer in the semiarid western Rio Grande Plains of Texas.

Increases in canopy cover of preferred annuals in March following discing in October were counterbalanced on the majority of sampling dates by reduced canopy cover of perennials preferred by white-tailed deer and I accepted the hypothesis that canopy cover of preferred perennials is reduced by frequent discing. Canopy cover of preferred perennials was also reduced by discing only once in 1990, and remained lower (P<0.05) than on controls throughout

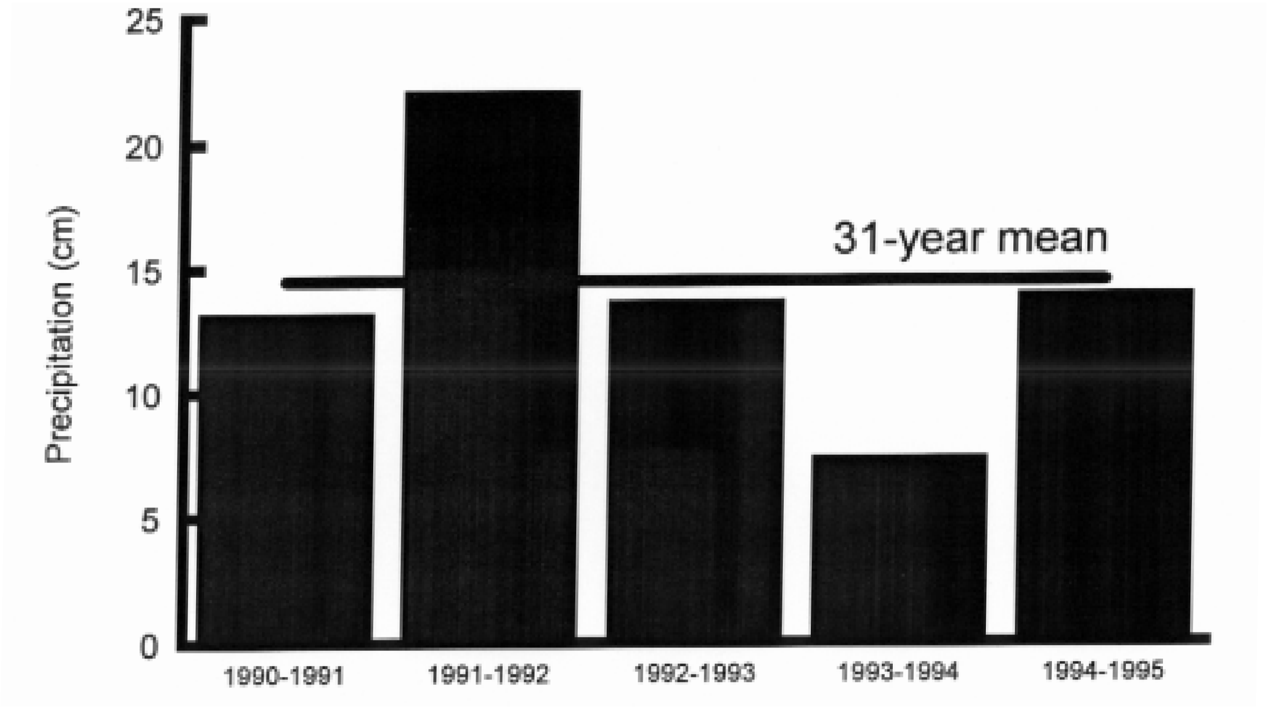

Fig. 1. Rainfall (cm) during the 6-month period from discing in October to sampling in March 1990–1995 and mean rainfall during October-March 1931–1962 (Thompson et al. 1972), El Tecomate Ranch, Starr County, Tex.

the 5 years of study. Consequently, I also rejected the hypothesis that discing only once allows reestablishment of perennial forbs resulting in greater total canopy cover of annual and perennial forbs preferred by deer.

Soil disturbance by discing is not recommended as a habitat improvement practice in the semiarid western Rio Grande Plains of Texas if the objective of management is to increase canopy cover of forbs preferred by white-tailed deer. Although preferred annuals and moderately palatable species (other species eaten by deer) were increased in March during a 4-year period following a single discing event in October, increasing annual forbs at the expense of preferred perennial forbs is not a desirable management strategy. Perennial forbs constitute a more stable food source for deer on a year-long basis than do annual forbs (Chamrad et al. 1979). Additionally, perennial forbs generally constitute a much greater proportion of deer diets than annual forbs. On the Welder Wildlife Refuge in eastern south Texas, perennial forbs composed 17% of deer diets by volume compared to 40% for annual forbs. Virtually all treatments increased unpalatable forbs, which is another important undesirable result of discing.

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Reclaiming Russian knapweed infested rangeland

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Abstract

Russian knapweed [*Acroptilon repens* (L.) DC.] is a creeping, perennial, unpalatable, noxious weed that infests thousands of rangeland and pasture hectares in the western U.S. often forming monocultures. Chemical or mechanical control of Russian knapweed usually is temporary allowing re-invasion of the weed over time. Our objective was to determine whether combining chemical or mechanical methods with seeding of perennial grasses would reclaim Russian knapweed infested areas more effectively than any of the treatments applied alone. Five suppression treatments combined with 5 seeded perennial grasses were evaluated to reclaim Russian knapweed infested site.

Two years after suppression treatments were done, clopyralid + 2,4-D + seeded grasses controlled 66 to 93% of Russian knapweed whereas clopyralid + 2,4-D applied alone controlled only 7% of Russian knapweed. Glyphosate + 'Critana' thickspike wheatgrass [*Elymus lanceolatus* (Scribn. & Sm.) Gould] controlled 36% of Russian knapweed 2 years after treatment (YAT) while glyphosate + 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], 'Bozoisky' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski], or 'Sodar' streambank wheatgrass [*Elymus lanceolatus* (Scribn. & Sm.)] increased Russian knapweed growth 1.5, 2, and 1.6-fold, respectively. Glyphosate applied alone tripled Russian knapweed growth. Metsulfuron + streambank wheatgrass controlled 61% of Russian knapweed 2 years after treatments were applied while metsulfuron applied alone controlled 40% of Russian knapweed. Mowing was ineffective and mowing + crested wheatgrass increased Russian knapweed growth about 2-fold. Clopyralid + 2,4-D + streambank wheatgrass yielded 6, 48, and 18 times more seeded grass than metsulfuron treated, mowed, or non-treated control plots seeded with streambank wheatgrass. Clopyralid + 2,4-D + streambank wheatgrass, while expensive ($262 ha^{-1}), was the best treatment combination because it controlled Russian knapweed effectively while the sod-forming grass established well and helped to prevent re-invasion by the weed.

Key Words: rangeland weed control, IPM, integrated weed management, cultural control

Resumen

"Russian Knapweed" [*Acroptilon repens* (L.) DC.] es una maleza perenne, rastrera no apetecida por el ganado y tóxica que infesta miles de hectáreas de pastizales y praderas del oeste de U.S. y a menudo forma monocultivos. El control químico y mécanico de "Russian Knapweed" es temporal permitiendo con el tiempo la reinvasión de la maleza. Nuestro objetivo fue determinar si la combinación de métodos químicos y mecánicos con la siembra de zacates perennes sería mas efectiva para recuperar áreas infestadas de "Russian Knapweed" que con la aplicación individual de cualquiera de los tratamientos. Se evaluaron 5 tratamientos de supersión combinados con la siembra de 5 zacates perennes para recuperar un sitio infestado de "Russian Knapweed".

Dos años después de la aplicación de los tratamientos de supresión, el tratamiento de "Clopyralid" + "2,4-D" + siembra de zacates controló del 66 al 93% del "Russian Knapweed" mientras que "Clopyralid" + "2,4-D" solo controló el 7% del "Russian Knapweed". Dos años después de aplicar el tratamiento (YAT) de "Glyphosate" + 'Critana' "Thickspike wheatgrass" [*Elymus lanceolatus* (Scribn. & Sm.) Gould] controlo 36% del "Russian Knapweed" en tanto "Glyphosate" + 'Hycrest' "crested wheatgrass" [*Agropyron cristatum* (L.) Gaertn.], 'Bozoisky' "Russian wildrye {Psathyrostachys juncea (Fisch.) Nevski] o 'Sodar' "streambank wheatgrass" [*Elymus lanceolatus* (Scribn & Sm.)] incrementaron el crecimiento del "Russian Knapweed" en 1.5, 2 y 1.6 veces respectivamamante. El "Glyphosate" aplicado solo triplico el crecimiento del "Russian Knapweed". Dos años después de aplicado el "Metsulfuron" + "streambank wheatgrass" controló el 61% del "Russian Knapweed" en tanto que el "Metsulfuron" aplicado solo controló el 40% del "Russian Knapweed". La siega fue inefectiva y la siega + "crested wheatgrass" incrementaron el crecimiento del "Russian Knapweed" en aproximadamente 2 veces. "Clopyralid" + "2,4-D" + "streambank wheatgrass" rindió 6, 48 y 18 veces más del zacate sembrado que las parcelas tratadas con "Metsulfuron", segadas o no tratadas (control) y sembradas con "streambank wheatgrass". La combinación de "Clopyralid" + "2,4-D" + "streambank wheatgrass", aunque cara ($262 ha^{-1}), fue la mejor porque controló el "Russian Knapweed" efectivamente mientras los zacates formadores de césped se establecieron bien y ayudaron a prevenir la reinvasión de la maleza.

Russian knapweed [*Acroptilon repens* (L.) DC] is a creeping, deep-rooted, aggressive, perennial weed considered nox-

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ious in 21 of the United States (Maddox et al. 1985). It is invasive and can rapidly colonize an area due to its fast growth and extensive root system. It also exhibits allelopathic characteristics (Fletcher and Renney 1963, Watson and Renney 1974, Muir and Majak 1983, Stevens and Merrill 1985) and tends to form dense, monocultures (Watson 1980). Its bitter taste usually deters grazing livestock, however, fresh or dried Russian knapweed is toxic to horses, causing equine nigropallidal encephalomalacia, a fatal neurological disorder (Young et al. 1970).

Control of Russian knapweed typically has been by mechanical, chemical, or cultural means used alone. Control of Russian knapweed or other noxious weeds on rangeland is difficult because of vast area, uneven topography, and lower land value compared to cropland. Although chemical control of Russian knapweed is effective, it is costly, non-target organisms must be considered, groundwater contamination must be avoided, and treated areas must be monitored and re-treated for weeds recurring from vegetative reproduction and viable seeds remaining in the soil. Russian knapweed often forms monocultures and successful chemical control may result in bare ground, which is as unproductive as the Russian knapweed infestations.

Plant competition can be used to complement other weed control methods (Bottoms et al. 1996). After several years, cereal crops planted in monoculture or crop/fallow rotation provided competition to control Russian knapweed (Watson 1980). Four years of winter rye (*Secale cereale* L.) or wheat (*Triticum aestivum* L.) monoculture decreased Russian knapweed populations 99 and 78% when crops were harvested for silage or grain, respectively (Sulima 1968). Russian knapweed is sensitive to light competition (Dall'Armellina and Zimdahl 1988). Flower production and root and shoot dry matter declined as light intensity was decreased while leaf area increased. Whitson et al. (1993) showed 'Ephraim' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], 'Oahe' intermediate wheatgrass [*Agropyron intermedium* (Host.) Beauv.], and 'Bozoisky' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] established in Russian knapweed stands without initial herbicide suppression at 20, 45, and 40% cover, 2 years after seeding. Perennial weed suppression is essential for successful grass establishment in integrated weed management. Unfortunately, little research has been conducted on integrated management of Russian knapweed. However, herbicide application followed by perennial grass seeding controlled 88 to 93% of leafy spurge (*Euphorbia esula* L.) 4 years after the combined treatments were invoked (Whitson et al. 1989). Seeding of competitive grasses in combination with herbicide and fertilizer treatments has been successful for long-term control of leafy spurge (Biesboer et al. 1993).

Herbicides chosen for Russian knapweed suppression on rangeland should include consideration of efficacy, residual activity, potential grass injury, sensitive habitat effects, and cost. Grasses chosen for long-term Russian knapweed management must exhibit adaptability to soil and climate, ease of establishment, competitiveness with weeds, palatability, nutritional value, good dry matter productivity, and stand longevity (Asay et al. 1991). The objective of this study was to determine whether combining suppression treatments with seeding of perennial grasses more effectively reclaimed Russian knapweed infested rangeland better than either method applied alone.

Materials and Methods

A field experiment was established in 1993 at Shoshoni, Wyo. on abandoned farm ground that was infested with Russian knapweed. The experiment was conducted for 3 years. The elevation was 1,469 m and the average annual precipitation was 22.5 cm. The soil was a Tipperary-Trook loamy sand (mixed, mesic Typic Torripsaminents—coarse-loamy, mixed mesic Typic Claciorthids) underlain by interbedded sandstone and varicolored shale of the Tertiary Wind River Formation; 89% sand, 4% silt, 7% clay with 1.1% organic matter and 8.0 pH. The 5 by 5 factorial experiment was arranged in a split block design and treatment combinations were replicated 4 times. Main plots were 9 by 30 m and were methods used to suppress Russian knapweed. Suppression treatments included no treatment, mowing, clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) + 2,4-D [(2,4-dichlorophenoxy)acetic acid], metsulfuron (methyl 2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]amino]sulfonyl]benzoate), or glyphosate [N-(phosphonomethyl)glycine]. Clopyralid + 2,4-D (0.3 + 1.7 kg ai ha^{-1}, sprayed at 225 liters ha^{-1}) and metsulfuron (42 g ai ha^{-1} + 0.25% v/v non-ionic surfactant, sprayed at 225 liters ha^{-1}) were applied when Russian knapweed was in the late bloom stage on 9 July, 1993. Sequential treatments of glyphosate (1.1 kg ai ha^{-1} + 1.1 kg ha^{-1}, sprayed at 94 liters ha^{-1}) were applied in the bud stage and again to remaining live plants on 11 June, 1993 and 7 August, 1993, respectively. All herbicides were sprayed with a CO_2 pressurized backpack sprayer. Sequential mowings occurred in the bud stage on 15 June, 1993 and to regrowth on 18 August, 1993.

In November, 1993, main-plots were split into six, 9 by 6 m sub-plots. Each sub-plot was rototilled to a 15-cm depth, then 1 perennial grass species was seeded with a rangeland drill. In addition to a non-seeded control treatment, 'Bozoisky' Russian wildrye grass, 'Hycrest' crested wheatgrass, 'Sodar' streambank wheatgrass, and 'Critana' thickspike wheatgrass were sown at 9, 11, 11, and 12 kg pure live seed ha^{-1}, respectively. These grasses were chosen because of their positive characteristics relative to the objectives of this study. Crested wheatgrass is easy to establish, resistant to drought and cold, and is valued for its productivity and nutritional properties in early spring (Asay et al. 1991). Thickspike and streambank wheatgrasses are similar, native, perennial grasses that often have been used in disturbed site renovation (Anonymous 1984). They are drought resistant, establish easily because of robust seedling vigor, produce fine leaves, and form tight sod under dry rangeland conditions. Sod-forming grasses are good choices for revegetation when noxious weeds are a factor for site rehabilitation (Callihan and Evans 1991). Russian wildrye is drought resistant and the cultivar ‘Bozoisky’ has greater seedling vigor than other cultivars (Asay et al. 1991). Russian wildrye has dense basal leaves with high nutritive value. It is noted for early spring productivity and retains higher nutritive value during late summer and fall than many other grasses.

Each of the 120 sub-plots representing an experimental unit was a combination of 1 suppression treatment and 1 seeded grass treatment. Treatments to suppress Russian knapweed and seeding of perennial grasses were done only during 1993 with no further management input. The outcome was evaluated in 1994 and 1995.

Data were collected twice during 1994 and 1995. Percent cover of each species was determined in late spring to measure the effectiveness of Russian knapweed suppression and seeded grass establishment. Canopy cover was determined by the Levy and Madden (1933) point method of pasture analysis. Biomass of each species was determined in late summer.

Baseline data were collected 8–10 June 1993 and used as a basis to monitor changes resulting from the various management systems. Data were collected in the same locations in each plot at about the same time in 1993, 1994, and 1995, after all vegetation had emerged and Russian knapweed was in the vegetative to early bud growth stage. Biomass was harvested in August, 1994 and 1995. Above ground vegetation was removed by clipping four, 0.25 m^2 quadrats in each sub-plot, taking care not to harvest along permanent transects. Clippings were separated by species and oven-dried at 35°C for 48 hours to a constant weight.

Analysis of variance (ANOVA) was used to compare 2 main effects: suppression treatments as main plots, seeded perennial grasses as the split plot, and subsequent interactions. Percent cover data were arcsine square root transformed and all weight measurements were cube root transformed to stabilize variance; however, original values are reported. Residual plots of transformed data indicated no violations of the assumptions associated with ANOVA. Means for suppression treatments, seeded grass species, and interactions were separated using Fisher's protected least significant difference (LSD; $\alpha = 0.05$). The expense ha^{-1} of each treatment combination was calculated and compared. Only costs of herbicides or mowing plus grass seed were used because application and seeding costs vary substantially.

Data from 1994 and 1995 were analyzed separately because of varying climatic conditions at the site. Vegetation varied substantially from year to year because 1994 was the worst drought in recorded history while 1995 was the second highest precipitation on record.

Results and Discussion

Russian knapweed baseline cover ranged from 37 to 40% and did not differ among suppression treatments before they were applied (data not shown, Benz 1997). In 1994, all herbicides controlled Russian knapweed better than mowing or the non-treated control (Table 1). Russian knapweed emerged earlier in mowed plots than in all plots treated with a herbicide or in non-treated control plots (data not shown, Benz 1997). Mowing may have altered shoot apical dominance causing more rapid emergence the following spring. Russian knapweed was suppressed best by clopyralid + 2,4-D (98% decrease in cover) and metsulfuron (99% decrease in cover). Plots treated with clopyralid + 2,4-D or metsulfuron in 1993 yielded about 75% less Russian knapweed in 1994 than glyphosate treated plots and 85% less than in mowed or non-treated control plots (Table 1). Under average weather conditions, the best opportunity for grasses to establish the year following seeding would occur where Russian knapweed was adequately controlled. Drought in 1994 interfered with grass establishment in all plots. Weather conditions will influence grass establishment even where noxious weeds are controlled adequately. For example, a second experiment was conducted simultaneously near Mead, Colo. and although Russian knapweed was controlled with clopyralid + 2,4-D and metsulfuron similarly to that observed at the Wyo. site, seedling wheatgrasses were killed in 2 of 4 replications because of cold temperatures. Killed grass seedlings were in replications located in the bottom of a draw and had emerged in late winter apparently because of better soil moisture conditions than the 2 replications located on a ridge top where grasses had not yet emerged. Seedling grasses in the draw did not survive –20 °C temperatures.

When weather conditions inhibit grass establishment, surviving seed will emerge later after conditions become suitable for germination. The best opportunity for grass establishment over time in Russian knapweed infested sites would occur where weeds are controlled adequately for the longest period. In 1995, 2 years after treatment (YAT), there was 13 times more Russian knapweed cover in glyphosate treated, mowed, and non-treated control plots than in clopyralid + 2,4-D plots (4%) and nearly 3 times more than in metsulfuron treated plots (18%; data not shown, Benz 1997). Long term control from clopyralid + 2,4-D (92% decrease in cover) was evident 2 years after treatment while glyphosate showed none. Metsulfuron decreased cover of Russian knapweed by 99% after 1 year but only by 65% after 2 years.

Russian knapweed growth in 1995 was influenced by the interaction of the suppression treatments and the seeded grass species. Any grass species seeded after Russian knapweed was suppressed with clopyralid + 2,4-D, produced 66 to 93% less Russian knapweed biomass than when no grass was sown (Table 2). Clopyralid + 2,4-D plus any seeded perennial grass were the only combinations to produce less Russian knapweed consistently compared to plots seeded with grass but without suppression. Metsulfuron combined with streambank wheatgrass produced the least Russian knapweed (274 kg ha^{-1}). Among plots sprayed with metsulfuron, those seeded with streambank wheatgrass or Russian

Table 1. Russian knapweed cover and biomass in 1994 as influenced by suppression treatments averaged over all seeded grasses.

Treatment	Rate	Russian knapweed	
	(kg ha^{-1})	(% cover)[1]	(kg ha^{-1})[1]
Clopyralid	0.3		
+ 2,4-D	+ 1.7	0.7 c	20 c
Glyphosate	1.1		
(6-93 + 8-93)	+ 1.1	4 b	72 b
Metsulfuron[2]	0.042	0.2 c	16 c
Mowing	0	43 a	117 a
(6-93 + 8-93)	0		
Control	0	43 a	117 a

[1]Cover data were analyzed as arcsine square root transformations and biomass analyzed as cube root transformations, but are presented as original values. Means followed by the same letter do not differ, LSD (P>0.05).
[2]Non-ionic surfactant added at 0.25% v/v

Table 2. The influence of suppression treatments interacting with seeded grasses on Russian knapweed biomass production in 1995.

		Russian knapweed biomass				
Treatment	Rate	Crested wheatgrass	Russian wildrye	Streambank wheatgrass	Thickspike wheatgrass	No grass control
	(kg ha^{-1})	(kg ha^{-1})[1]				
Clopyralid + 2,4-D	0.3 + 1.7	83 C c	152 C d	43 D c	193 B c	567 A b
Glyphosate (6-93 + 8-93)	1.1 + 1.1	896 C ab	1546 AB a	1149 BC a	362 D b	1836 A a
Metsulfuron[2]	0.042	523 A b	523 A c	274 C b	373 B ab	371 B c
Mowing (6-93 + 8-93)	0 0	1120 A a	1112 A ab	1047 A a	809 A a	896 A ab
Control	0	586 AB b	718 A b	700 AB a	564 B ab	609 AB b

[1]Data were analyzed as cube root transformations but are presented as original values. Use upper case letters to compare means within a row and lower case letters to compare means within a column. Means followed by the same letter do not differ, LSD (P>0.05).
[2]Non-ionic surfactant added at 0.25% v/v

wildrye produced 28 and 61% less Russian knapweed biomass than plots seeded with these grasses but without suppression treatments. Over 5 times more Russian knapweed was harvested from glyphosate-only treated plots (1,836 kg ha^{-1}) than from plots where glyphosate was combined with thickspike wheatgrass (362 kg ha^{-1}). Glyphosate provided no advantage over mowing except in thickspike wheatgrass plots where half as much Russian knapweed was harvested than in mowed plots (362 vs 809 kg ha^{-1}). The characteristics of thickspike wheatgrass as a revegetation species may have enhanced this combination. It forms tight sod under dry rangeland conditions, has robust seedling strength, and performs well in low fertility or eroded sites (Asay et al. 1991). Mowing was a poor suppression treatment and did not control Russian knapweed effectively in any year. In all plots seeded with perennial grasses where mowing was the suppression treatment, 4 to 24 times more Russian knapweed was harvested than in these same grass plots where clopyralid + 2,4-D was used. Russian knapweed shoot apical dominance could have changed because of mowing, which may have caused more shoots per unit area and decreased the opportunity for seeded grasses to establish. In plots where little Russian knapweed biomass was harvested, the suppression treatment was effective enough to allow successful establishment and growth of seeded grass, which kept Russian knapweed from re-invading.

Our results indicate that glyphosate should be re-applied the year following the first treatment, metsulfuron may need to be re-applied 2 years after the first treatment, and clopyralid + 2,4-D may provide sufficient suppression so re-application would not be necessary.

Seeded grass cover in 1994 was less than 3% for all species. Poor germination and establishment was influenced by severe drought in 1994. Seeded grasses were established, however, by the time cover data were collected in spring, 1995. Herbicides suppressed Russian knapweed better in 1994 than mowing or no treatment. Herbicides helped seeded grass establish by suppressing Russian knapweed and decreasing its competition with seeded grasses. A suppression treatment by seeded grass species interaction effect in 1994 and 1995 showed that herbicides aided seeded grass establishment better than mowing. In 1994 for example, crested wheatgrass cover in plots treated with clopyralid + 2,4-D, glyphosate, or metsulfuron ranged from 4 to 6% and crested wheatgrass cover in these plots was 15 times greater than in mowed and nontreated control plots seeded with this grass (data not shown, Benz 1997). In 1995, all plots where Russian knapweed was suppressed with a herbicide and then seeded with a perennial grass, had 3 to 18 times greater seeded grass cover than mowed or non-treated control plots that were seeded with a perennial grass except where glyphosate was combined with Russian wildrye (Table 3). For example, grass cover in metsulfuron treated plots seeded with crested wheatgrass (57%) was nearly 4 times more than grass cover in plots seeded with crested wheatgrass that did not receive a suppression treatment (15%) and over 8 times more grass cover than in mowed plots seeded with crested wheatgrass (7%).

In 1995, seeded grass biomass was influenced by suppression treatments interacting with seeded grass species. In general, plots where Russian knapweed was suppressed with a herbicide and then seeded with crested wheatgrass had more grass biomass in 1995 than where other perennial grasses were sown. In plots treated with glyphosate or metsulfuron, crested wheatgrass biomass was 3 to 20 times and 15 to 100 times greater, respectively, than where other grasses were sown (Table 4). This effect most

Table 3. The influence of suppression treatments interacting with seeded grasses on seeded grass cover in 1995.

		Seeded grass cover				
Treatment	Rate	Crested wheatgrass	Russian wildrye	Streambank wheatgrass	Thickspike wheatgrass	No grass control
	(kg ha^{-1})	(%)[1]				
Clopyralid + 2,4-D	0.3 + 1.7	55 A ab	5 C a	15 B a	18 B a	0 D a
Glyphosate (6-93 + 8-93)	1.1 + 1.1	46 A b	3 C ab	18 B a	11 B b	0 D a
Metsulfuron[2]	0.042	57 A a	5 C a	11 B a	10 B b	0 D a
Mowing (6-93 + 8-93)	0 0	7 A d	0 B c	1 B b	1 B c	0 B a
Control	0	15 A c	1 B bc	2 B b	1 B c	0 C a

[1]Data were analyzed as arcsine square root transformations but are presented as original values. Use upper case letters to compare means within a row and lower case letters to compare means within a column. Means followed by the same letter do not differ, LSD (P>0.05).
[2]Non-ionic surfactant added at 0.25% v/v

Table 4. The influence of suppression treatments interacting with seeded grasses on harvested seeded grass biomass in 1995.

Treatment	Rate	Harvested grass biomass: Crested wheatgrass	Russian wildrye	Streambank wheatgrass	Thickspike wheatgrass	No grass control
	(kg ha^{-1})	(kg ha^{-1})[1]				
Clopyralid + 2,4-D	0.3 + 1.7	335 A b	3 C a	242 AB a	78 B ab	0 C a
Glyphosate (6-93 + 8-93)	1.1 + 1.1	454 A b	21 C a	69 B ab	159 B a	0 C a
Metsulfuron[2]	0.042	634 A a	6 B a	40 B bc	36 B bc	0 C a
Mowing (6-93 + 8-93)	0 0	18 A c	6 A a	5 A d	6 A c	0A a
Control	0	44 A c	0 B a	13 AB cd	8 AB c	0 B a

[1]Data were analyzed as cube root transformations but are presented as original values. Use upper case letters to compare means within a row and lower case letters to compare means within a column. Means followed by the same letter do not differ, LSD (P>0.05).
[2]Non-ionic surfactant added at 0.25% v/v

likely was caused by drought in 1994 when crested wheatgrass was the only perennial grass to grow in the dry environment. In plots where Russian knapweed was suppressed with clopyralid + 2,4-D and then seeded with crested wheatgrass, 100 times more grass biomass (335 kg ha^{-1}) was produced than in plots seeded with Russian wildrye (3 kg ha^{-1}), and 4 times more than those seeded with thickspike wheatgrass (78 kg ha^{-1}). Plots treated with clopyralid + 2,4-D then seeded with crested wheatgrass or streambank wheatgrass had similar yields in 1995. The clopyralid + 2,4-D plus streambank wheatgrass combination had less Russian knapweed than all other plots treated with clopyralid + 2,4-D or seeded with streambank wheatgrass. The long term Russian knapweed control provided by clopyralid + 2,4-D allowed vigorous seeded grass growth among the wheatgrasses in 1995. The similar yields between crested wheatgrass and streambank wheatgrass in plots treated with clopyralid + 2,4-D may have been at least partially caused by minor injury to crested wheatgrass from the herbicide. The clopyralid + 2,4-D label states that crested wheatgrass may be injured under drought conditions. The similarity between crested wheatgrass and streambank wheatgrass yields in plots treated with clopyralid + 2,4-D is in sharp contrast to those plots treated with glyphosate or metsulfuron. It is clear that plots originally treated with glyphosate or metsulfuron needed retreatment in 1995 whereas those treated with clopyralid + 2,4-D may not have needed retreatment until 1996, if at all. Effective, long term control of weeds, especially perennial, noxious weeds, is an important consideration when designing integrated weed management systems for rangelands.

Plots treated with glyphosate yielded 4 times more thickspike wheatgrass biomass (159 kg ha^{-1}) than those treated with metsulfuron (36 kg ha^{-1}) and 28 times more than mowed plots (6 kg ha^{-1}). Also, suppression treatments that controlled Russian knapweed best did not necessarily provide the most seeded grass production. Metsulfuron treated plots produced about twice as much crested wheatgrass biomass (634 kg h^{-1}) than those treated with clopyralid + 2,4-D (335 kg ha^{-1}) and 14 times more than in the non-treated control plots (44 kg ha^{-1}), although over 6 times more Russian knapweed biomass was harvested from metsulfuron plus crested wheatgrass plots than from clopyralid + 2,4-D plus crested wheatgrass plots. Again, this effect may be a reflection of minor crested wheatgrass injury from clopyralid + 2,4-D caused under drought. Bozoisky Russian wildrye did not establish well at this site, however it was successful in other Wyoming revegetation studies (Ferrell et al. 1992).

The most expensive treatment combination was clopyralid + 2,4-D plus thickspike wheatgrass ($278/ha) and the least expensive was mowing plus crested wheatgrass ($70 ha^{-1}; Fig. 1). The combination of metsulfuron plus crested wheatgrass resulted in the greatest grass biomass per dollar invested in the management system, but it left as much Russian knapweed in the plot area as the no suppression plus crested wheatgrass combination 2 years after treatment. Glyphosate plus crested wheatgrass caused a similar result. Clopyralid + 2,4-D was the most expensive suppression treatment ($67 ha^{-1}), but controlled the most Russian knapweed for the longest period of time and retreatment may not have been necessary. Plots treated with glyphosate ($61 ha^{-1}) or metsulfuron ($49 ha^{-1}) would have to be retreated thus adding to the expense of those treatment combinations. Glyphosate would be a poor choice for retreatment after grass establishment because it is non-selective. Our study indicates that clopyralid + 2,4-D plus streambank

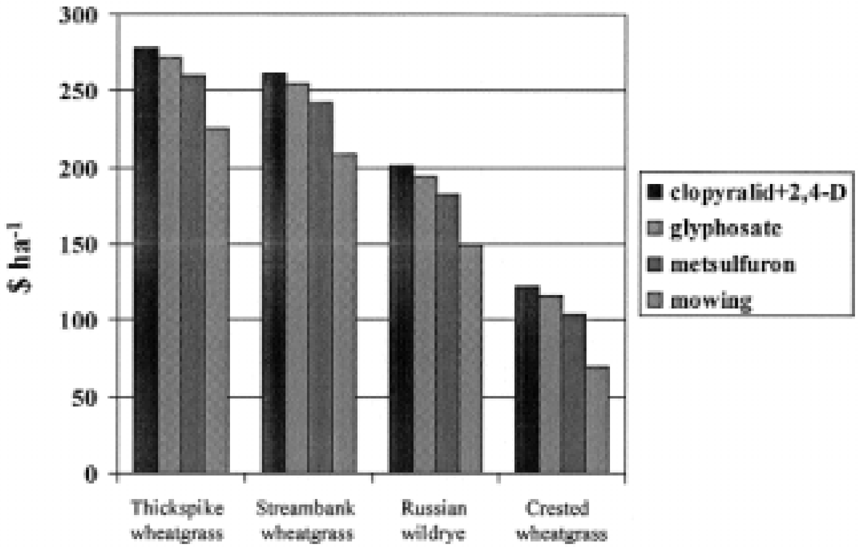

Fig.1. Cost comparison of the suppression treatments combined with seeded grasses. Only the cost of herbicides or mowing plus grass seed were used.

wheatgrass, while expensive ($262 ha^{-1}), provided the best long-term Russian knapweed control and good grass establishment, although grass establishment was not better than clopyralid + 2,4-D plus crested wheatgrass. Crested wheatgrass is a bunchgrass and most productive early in the growing season. Streambank wheatgrass is a sod-forming species that retains its productivity and nutritive value later in the growing season than crested wheatgrass. Sod-forming grasses are considered good choices as part of a long-term noxious weed management system. The best treatment combination resulting from our study was clopyralid + 2,4-D plus streambank wheatgrass and would be particularly well suited to areas where only native grasses are desired. Given the ease of establishment of crested wheatgrass, especially under drought conditions that are common in the Intermountain West, a sound recommendation to reclaim Russian knapweed infested rangeland or pastures would be clopyralid + 2,4-D plus streambank wheatgrass plus crested wheatgrass. Both grass species would establish easily and crested wheatgrass would provide early season grazing opportunities and competition with Russian knapweed that was recovering from suppression, whereas sod-forming streambank wheatgrass would provide long-term competition with Russian knapweed to prevent its re-invasion and provide grazing later into the season.

Previous studies (Christianson et al. 1994, Ferrell et al. 1995, Whitson et al. 1989) showed that integration of treatments is more effective than using single weed control techniques for perennial weeds. Our data support the hypothesis that a combination of a suppression treatment plus a seeded perennial grass was more effective than either method alone to reclaim Russian knapweed infested rangeland. The grasses used in our research needed initial suppression of Russian knapweed to permit establishment, and herbicides worked better than mowing.

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Canopy analysis as a technique to characterize defoliation intensity on Sandhills range

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Abstract

Characterization of relationships between grazing and vegetation responses is difficult. Rapid and accurate measurement of pasture canopy characteristics would help clarify these relationships if canopy changes are directly related to grazing variables. The objectives of this study were (1) to evaluate use of the LI-COR LAI-2000 for quantification of changes in canopy density and architecture in response to defoliation by cattle, (2) to determine if changes in leaf area index (LAI) measured with the LAI-2000 are related to stocking rate, and (3) to determine advantages and drawbacks of the LAI-2000 for monitoring grazing impacts on canopy density and architecture. Leaf area index and mean foliage tilt angle were measured before and after defoliation by cattle (Bo*s taurus L.)* in June, July, and August under 9 grazing treatments on Nebraska Sandhills range. Differences in LAI could be attributed to certain grazing treatments at various points throughout the season. Grazing treatment had little impact on mean foliage tilt angle. Change in LAI (ΔLAI) had a significant negative relationship with stocking rate (P≤0.0001). The relationship detected for ΔLAI versus stocking rate predicted LAI reductions of between 0.14 and 0.40 for the range of stocking rates studied; stocking rate accounted for 62% of the decrease in LAI caused by grazing. When configured for the Sandhills canopy, the LAI-2000 provided a rapid and precise method for quantification of the degree of defoliation associated with grazing.

Key Words: LI-COR LAI-2000, leaf area index, foliage tilt angle

Resumen

La caracterización de las relaciones entre el apacentamiento y la respuesta de la vegetación es difícil. Si los cambios de la copa de la pradera estan directamente relacionados a variables de apacentamiento, la medición rápida y acertada de las características de la copa podría ayudar a clarificar estas relaciones. Los objetivos de este estudio fueron: (1) evaluar el uso del LI-COR LAI-2000 para cuantificar los cambios en la densidad y arquitectura de la copa en respuesta a la defoliación por ganado, (2) determinar si los cambios en el índice de área foliar (IAF) medidos con el LAI-2000 estan relacionados a la carga animal y (3) determinar las ventajas y desventajas del LAI-2000 para monitorear los impactos del apacentamiento en la denisidad y arquitectura de la copa. Se midieron el índice de área foliar y el ángulo promedio de inclinacion del forraje antes y después de la defoliación por ganado (*Bos taurus* L.) durante Junio, Julio y Agosto bajo 9 tratamientos de apacentamiento en los pastizales "Nebraska Sandhills". Diferencias en IAF pudieron ser atribuidas a ciertos tratamientos de apacentamiento en varios puntos a través de la estación. Los tratamientos de apacentamiento tuvieron poco impacto en el ángulo promedio de inclinación del forraje. Los cambios en IAF (ΔIAF) tuvieron una relación negativa significativa con la carga animal (P≤0.0001). La relación detectada para ΔIAF versus carga animal predijó reducciones de IAF de entre 0.14 y 0.40 para el rango de cargas animal estudiadas. La carga animal explicó el 62% de la disminución del IAF causada por apacentamiento. Cuando el LAI-2000 fue configurado para la copa de los "Sandhills" el LAI-2000 proveyó un método rápido y preciso para cuantificar el grado de defoliación asociado con el apacentamiento.

Proper herbage utilization is one of the most important considerations in range management and numerous methods have been developed for its measurement (Cook and Stubbendieck 1986). Many of these methods have been criticized because they estimate a quantity that is no longer present to measure directly and give only a rough approximation as to the degree of defoliation (Heady 1949, Heady and Child 1994, Sharp et al. 1994). Also, Hyder (1954) pointed out that sources of variation in site factors and plant communities within rangeland pastures cause uneven grazing distribution and prevent a direct plant physiological interpretation of utilization percentages. Alternative approaches proposed for several rangeland types measured utilization based on herbage residue rather than herbage removed (Bentley and Talbot 1951, Heady 1956, Bement 1969, Schmutz 1971). A desirable compromise, par-

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ticularly for research studies, would be a rapid, nondestructive method to accurately and precisely quantify a plant parameter that could be measured before and after a grazing event, and related directly to both stocking rate and defoliation impacts on plant function.

Brown and Blaser (1968) suggested that the development of the leaf area index (LAI) concept in pasture growth and management would bring together physical and physiological properties of plant communities to help clarify the complicated relationship between pasture growth and utilization. In a series of studies, Parsons et al. (1983a, 1983b) used LAI to maintain canopies of perennial ryegrass swards in 'leniently'-grazed (LAI = 3.0) and 'hard'-grazed (LAI = 1.0) conditions to determine the balance between photosynthesis, animal intake, and losses of vegetative matter. However, few measures of LAI have been reported for native range canopies.

We adapted a relatively new technology in nondestructive plant canopy analysis (Welles and Norman 1991) to quantify changes in canopy density (leaf area index) and architecture (mean foliage tilt angle) before and after defoliation by cattle for an array of grazing treatments on Sandhills range. Our objectives were (1) to evaluate use of the LI-COR LAI-2000[1] for quantification of canopy changes in response to defoliation by grazing herbivores, (2) to determine if changes in leaf area index (LAI) measured with the LAI-2000 are related to stocking rate, and (3) to determine advantages and disadvantages of the LAI-2000 for monitoring grazing impacts on canopy density and architecture.

Materials and Methods

Study Site

Data were collected June–October 1991 at the University of Nebraska Gudmundsen Sandhills Laboratory located 11 km northeast of Whitman, Neb. Soils are Valentine fine sands (mixed, mesic Typic Ustipsamments) derived from eolian sand parent material. Vegetation is dominated by mid and tallgrass including sand bluestem {*Andropogon gerardii* var. *paucipilus* (Nash) Fern.}, prairie sandreed {*Calamovilfa longifolia* (Hook.) Scribn.}, and little bluestem {*Schizachyrium scoparium* (Michx.) Nash}. Other species common at the site are prairie junegrass {*Koeleria macrantha* (Ledeb.) Schult.}, sand dropseed {*Sporobolus cryptandrus* (Torr.) Gray}, needle-and-thread (*Stipa comata* Trin. & Rupr.), hairy grama (*Bouteloua hirsuta* Lag.), western ragweed (*Ambrosia psilostachya* DC.), and sedges (*Carex* spp.).

Precipitation recorded for the periods Jan-March, April–September, and October–December 1991 were 111, 420, and 93 mm, respectively. These values represented 159%, 100%, and 133% of the 30-year average precipitation recorded at the NOAA site 10 km northeast of the Gudmundsen Laboratory (Reece et al. 1996).

Treatments

Grazing treatments consisted of 4 to 7-day, mid-month grazing periods in (1) June, (2) July, (3) August, (4) June and July, (5) June and August, (6) July and August, or (7) June, July, and August, (8) October, and (9) ungrazed controls (Table 1). Treatments were replicated 3 times over 24, 1.0-ha paddocks (Reece et al. 1996). Grazing treatments were applied to the same paddocks during 4 consecutive years beginning in 1988. Cattle were weighed after an overnight stand without food and water and allocated to treatments by weight. One animal unit (AU) was equal to 454 kg of yearling cattle. Seasonal stocking rates were set each year at 60% utilization of current year herbage as estimated in pastures grazed only in June. Seasonal stocking rates were equal among treatments and divided equally over multiple grazing periods. In 1991 the seasonal stocking rate was 1.62 AUM ha^{-1} and grazing periods were 3–4 days.

Three permanent 50-m transects were randomly located in each pasture and in 3 ungrazed areas contiguous to the pastures. Five, 1-m^2 quadrats were randomly located in permanent positions along each transect and used as the locations for canopy analysis measurements.

Canopy Analysis

Leaf area index and mean inclination of the foliage were measured indirectly at each of the 15, 1-m^2 quadrats in each pasture using the LAI-2000 immediately before (pre-grazing) and after (post-grazing) defoliation events in June, July, and August. These measurements were made whether or not a pasture was grazed at those times. Measurements were also made in ungrazed areas pre- and post-grazing. In October, pre-grazing measurements were made in all areas but since the canopy was senescent, post-grazing measurements were made only in pastures grazed at that time.

The LAI-2000 consists of an optical sensor and control box/datalogger. The sensor incorporates fisheye optics to project a hemispheric image of the canopy onto 5 silicon detectors that are arranged in concentric rings. The control box records the sensor's data and performs the calculations necessary for determining LAI and mean foliage tilt angle; standard errors are also calculated for both parameters. The technique combines a measurement of sky brightness from a leveled sensor above the canopy with a second measurement taken beneath the canopy with the sensor again viewing skywards. Attenuation of diffuse sky radiation is measured simultaneously at 5 zenith angles (7°, 23°,

Table 1. Treatment number, stocking rate/grazing period, and dates of mid-month grazing periods Gudmundsen Sandhills Laboratory, Whitman Neb., June–October 1991.

Treatment number	Stocking rate/ grazing period	Mid-month grazing periods Mid-June	Mid-July	Mid-August	Mid-October
	--(AUM ha^{-1})--	- - - - - - - - - (Grazing date/frequency) - - - - - - - - -			
(1)	1.62	X			
(2)	1.62		X		
(3)	1.62			X	
(4)	0.81	X	X		
(5)	0.81	X		X	
(6)	0.81		X	X	
(7)	0.54	X	X	X	
(8)	1.62				X
(9)	0				

[1]LI-COR, Inc., Box 4425, 4421 Superior St., Lincoln, Neb. 68504 U.S.A.

38°, 53°, 68°). The ratio of each ring's signals (below to above) is then assumed to be equivalent to the canopy's gap fraction (the fraction of sky visible through the canopy) at that ring's viewing angle. By measuring attenuation at several angles from the zenith, foliage orientation information can also be obtained (Welles and Norman 1991).

For this study, the LAI-2000 was configured to calculate LAI and mean tilt angle with 1 above-canopy and 5 below-canopy readings on the top-left to bottom-right diagonal of each of the 5 quadrats located along the 3 transects in each pasture. Thus, average LAI or mean tilt angle for a given pasture were each based on 15 separate determinations. Multiple below-canopy measurements are usually required to achieve a suitable spatial average for a site. A simple procedure was initially used to determine the number of below-canopy readings necessary for 95% confidence that the true LAI mean was within ±10% of the measured LAI. LAI determinations were made based on 6 below-canopy readings in 10 randomly selected areas then coefficients of variation determined as (standard error of the LAI measurements)/ average LAI. The coefficient was compared to published guidelines (LI-COR, Inc. 1993) to determine the number of below-canopy readings necessary.

The view of the sensor often needs to be restricted to mask out the operator or the sun. A canopy with large gaps may require a narrowed field of view so that gaps and canopy can be correctly integrated. Opaque masks that obscure 90°, 180°, 270°, or 315° can be placed onto the sensor to modify the field of view. View restriction to 45° was required for this study to mask the operator, and because the Sandhills canopy is heterogenous and has significant gaps (LI-COR, Inc. 1993). Also, the part of the canopy visible to the sensor should be shaded since the more sunlit leaves the sensor detects, the larger the underestimate of LAI. For this study, all measurements were made between 0430–0930 hours or 1630–2030 hours to take advantage of diffuse sunlight, and shadows cast by the operator that acted to shade the sensor and canopy when the sun was low in the sky. Slope effects on LAI estimates were minimized by choice of view cap (restriction to 45°) and by consistent orientation of the sensor along the contour for both below and above readings (LI-COR, Inc. 1993).

Data analysis

Pre- and post-grazing LAI and mean foliage tilt angle values were analyzed within months (June–October) using general linear models analysis of variance (SAS Institute Inc., 1990). Mean differences were separated using Fischer's protected LSD at P=0.05. Coefficient of variation (CV) and analysis of residual variation $\{\sigma^2_{Tmt*Blk} = \sigma^2_{Pasture}+(\sigma^2_{Sampling}/n)\}$ over grazing treatments within pre- and post-grazing measurements were calculated as indices of sample (n) adequacy (Kleinbaum and Kupper 1978). Sample number was considered adequate when the CV was less than 10%. Change in LAI (ΔLAI) was calculated for each pasture as the difference in LAI before and after each grazing use period:

$$\Delta LAI = LAI_{post\text{-}grazing} - LAI_{pre\text{-}grazing} \quad \textbf{(1)}$$

Analysis of variance revealed no date x stocking rate interaction so data were pooled over date for further analysis of the relationship between ΔLAI and stocking rate. Pearson correlation coefficients (SAS Institute, Inc. 1990) and associated asymptotic standard errors (ASE) were used to determine the strength of the relationship between ΔLAI and stocking rate for June to August grazing events. Custom (univariate) hypothesis tests were obtained to develop linear and quadratic components of a prediction model using the contrast statement in General Linear Models ANOVA (SAS Institute Inc., 1990).

Results and Discussion

Leaf Area Index

Within both pre- and post-grazing measurements, differences in leaf area index LAI could be attributed to certain grazing treatments at various points throughout the season (Fig. 1a, b, c, d). For example, pastures grazed in both June and August had lower LAI before the June grazing event than pastures grazed in June and July of previous

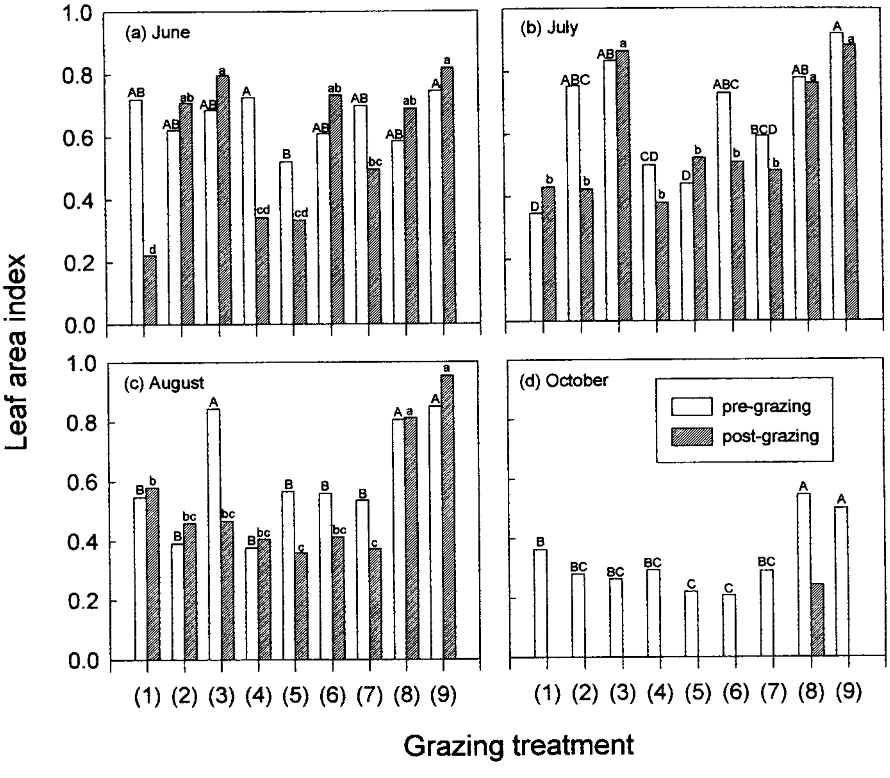

Fig. 1. Pre-grazing (means with upper case letters) and post-grazing (means with lower-case letters) leaf area index values for Sandhills range exposed to 8 grazing strategies or ungrazed, June–October 1991. Means with the same letter within pre-grazing or post-grazing measurements are not significantly different (P<0.05). Treatment designations: (1) grazed mid-June only; (2) grazed mid-July only; (3) grazed mid-August only; (4) grazed both mid-June and mid-July; (5) grazed both mid-June and mid-August; (6) grazed both mid-July and mid-August; (7) grazed mid-June, mid-July, and mid-August; (8) grazed mid-October only; (9) not grazed.

Table 2. Mean coefficients of variation (CV) and standard deviations (SD) for leaf area index (LAI) and mean foliage tilt angle (MTA) measured with the LI-COR LAI-2000, Gudmundsen Sandhills Laboratory, Whitman Neb., June–October 1991.

	June	July	August	October
	- (CV (SD), %)- - - - - - - - - - - - - - - - - - - -			
LAI				
pre-grazing	7.5 (0.5)	6.6 (0.7)	7.0 (0.9)	9.1 (3.5)
post-grazing	7.5 (1.6)	7.6 (1.1)	8.3 (1.4)	11.4
MTA				
pre-grazing	1.9 (0.5)	2.2 (0.9)	2.3 (0.7)	3.7 (1.4)
post-grazing	3.2 (1.5)	2.3 (0.7)	2.3 (0.6)	6.2

years, or ungrazed sites (Fig. 1a).

Canopy analysis with the LAI-2000 also allowed detection of differences in LAI as pastures entered the dormant season. As expected, ungrazed areas had higher LAI than any of the grazed pastures after the final grazing event in October (Fig. 1d). However, pastures grazed only in June (1) at the full seasonal stocking rate had higher LAI in October compared to pastures grazed twice at 1/2 the seasonal stocking rate in June and August (5) or in July and August (6, Fig. 1d).

Knight (1973) recognized the influence of leaf area on ecosystem processes, particularly primary productivity, and followed total green LAI of shortgrass range in Colorado over a single season. He reported LAI values between 0.1 and 0.6 and showed slightly higher leaf area attrition on heavily (0.7 ha per yearling month) versus lightly (1.4 ha per yearling month) grazed shortgrass pastures after 30 years of summer grazing (1 May to 31 October). Welles and Norman (1991) measured LAI between 1.0 and 3.5 for tallgrass prairie plots in Kansas. In this study, mean LAI measured with the LAI-2000 ranged between 0.75 and 1.0 for ungrazed Sandhills canopies from June through August (Fig. 1a, b, c). In grazed canopies, mean LAI values as low as 0.22 were measured (Fig. 1a).

Mean Foliage Tilt Angle

Grazing treatments had little impact on mean foliage tilt angle. Monthly mean foliage tilt angle decreased from a range of 62–69° in June to 56–64° in October. Decrease in foliage angle was most likely a result of continuous canopy senescence throughout the season as actively growing species changed from cool- to warm-season. Foliage angle values obtained in this study were similar to those reported by Smith et al. (1977) for foliage inclination angle of actively-growing western wheatgrass {*Pascopyron smithii* (Rydb.) A. Löve}. Average foliage inclination angles in that study were 68° and 66°, respectively, using the orthogonal projection and Fredholm integral equation methods.

Sample Adequacy

Coefficients of variation calculated for LAI and mean foliage tilt angle averaged over grazing treatments in June, July, or August were consistently less than 10% for LAI and 4% for tilt angles (Table 2). Coefficients of variation for both parameters increased as the canopy reached senescence but exceeded 10% only for post-grazing LAI measurements in October. Predicted residual variation (pasture + sampling) was reduced 64 ± 8.6% by a 15-fold increase in sample size (n = 1 to 15 LAI measurements per pasture) over all dates (Fig. 2). Increasing sample number to 30 LAI measurements per pasture only reduced predicted residual variation by an additional 6.7±2.3% over all dates.

ΔLAI versus Stocking Rate

The Pearson correlation coefficient between ΔLAI and stocking rate was –0.78 (ASE = 0.51). A significant ($P<0.001$) quadratic trend detected for ΔLAI versus stocking rate (Fig. 3) predicted decreases in LAI between 0.14 and 0.40 for the range of stocking rates studied June through August. Stocking rate accounted for 62% of the decrease in LAI after grazing events. Thus, ΔLAI measured with the LAI-2000 appears to have a moderate to strong relationship to stocking rate and would be useful as an index of pasture-level defoliation intensity of Sandhills canopies by cattle. Sequential, non-destructive measurements of canopy disappearance have been used previously to measure relative palatability of grasses and legumes under grazing. In one study, Stringer et al. (1995) compared non-destructive techniques to follow changes in canopy volume of space-planted, endophyte-free tall fescue (*Festuca arundinacea* Schreb.) plants as an indication of grazing activity and animal preference, but similar relationships were not studied in a solid sward or related to stocking rate.

Advantages and Drawbacks

Average measurement time per pasture using the LAI-2000 was 20 min., including time required to locate transect markers and move from quadrat to quadrat. In retrospect, analysis of residual variation indicated that as few as 10 LAI measurements per pasture may have been adequate for this rangeland type, further reducing measurement time per pasture. In contrast, leaf area measurements on shortgrass range reported by Knight (1973) using the nondestructive point-quadrat technique in 0.5-ha plots required 18 hours of labor for 1 LAI determination. Time required to complete 6 of the non-destructive techniques in the study by Stringer et al. (1995) ranged between 7 and 10 min. to set up and measure a single plant. For a seventh technique studied by Stringer et al. (1995), the table method, 2 persons could measure and record canopy diameter and height on 70 plants in 10 min. but the apparatus did not appear suited for easy transport between pastures, particularly in terrain such as that found in Sandhills range. In contrast, the LAI-2000 is lightweight, portable, and easily worn by a single operator while traversing large areas. The LAI-2000 also appears more suited for characterization of canopy responses to grazing in a heterogenous plant community such as that found on native range.

Canopy measurements were slower on mornings following a heavy dew since it was difficult to keep water droplets from falling on the sensor when below-canopy readings were made. Frequent stops were necessary to clean the sensor lens before measurements could be continued within a pasture. This difficulty could be circumvented by waiting until the dew dries, but by that time, the angle of the sun may be such that adequate

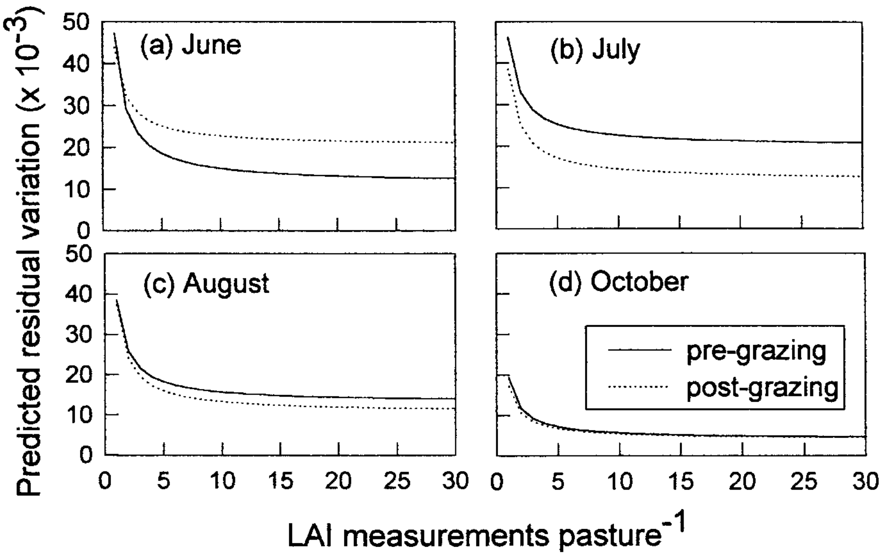

Fig. 2. Predicted residual variation for pre-grazing and post-grazing leaf area index (LAI) values based on between 1 and 30 LAI measurements per pasture (a) June, (b) July, (c) August, (d) October 1991.

shade becomes the limiting factor. Alternatively, measurements could be made only in the late afternoon and evening. Either of these options reduces the potential number of areas measured per day. In this study, it was possible to measure all 24 pastures and ungrazed areas within 36 hours of cattle removal.

Another relationship explored was the strength of the relationship between mean pasture production and mean pre-grazing pasture LAI obtained with the LAI-2000 June through October. Pasture production information had been obtained immediately prior to grazing for studies conducted in the same pastures (Reece et al. 1996). The Pearson correlation between pre-grazing pasture production and mean LAI was moderate, however, the prediction model developed to relate LAI to pre-grazing biomass accounted for less than 50% (r^2 = 0.43) of the variation in pasture production. Harmoney et al. (1997) compared predictive strength of several well-established indirect methods for estimation of pasture biomass to that of the LAI-2000 for homogeneous swards of warm- and cool-season grasses in Iowa. They reported an overall r^2 = 0.32 for the regression equation developed using LAI-2000 readings vs. r^2 = 0.61, 0.63, and 0.58 respectively for readings with the modified Robel pole, rising plate meter, and canopy height stick. Their conclusion was that established methods for biomass estimation had greater accuracy than the LAI-2000. Our results with this relationship on Sandhills range support their observation.

Conclusions

When configured for the Sandhills canopy, the LAI-2000 provided a rapid, precise method for quantification of foliage density reduction and recovery rates in response to grazing at different levels or dates throughout the season. Although reduction in whole-plant photosynthesis following defoliation is not necessarily proportional to leaf area or biomass removal, recovery of whole-plant photosynthetic capacity is dependent on the rate at which new photosynthetic surfaces are produced to an equal or greater extent than compensatory photosynthesis (Briske and Richards 1995). Thus, leaf area index LAI measurements could be made at closely-spaced intervals between defoliation events to determine leaf area recovery rates under different grazing treatments. This may be particularly useful in research studies where accurate and precise sampling is required to relate specific grazing treatments to vegetation response. While predictive strength of the relationship between LAI and pasture biomass was moderate at best in this study, further work is needed with the LAI-2000 in various native range canopy types to determine if LAI and

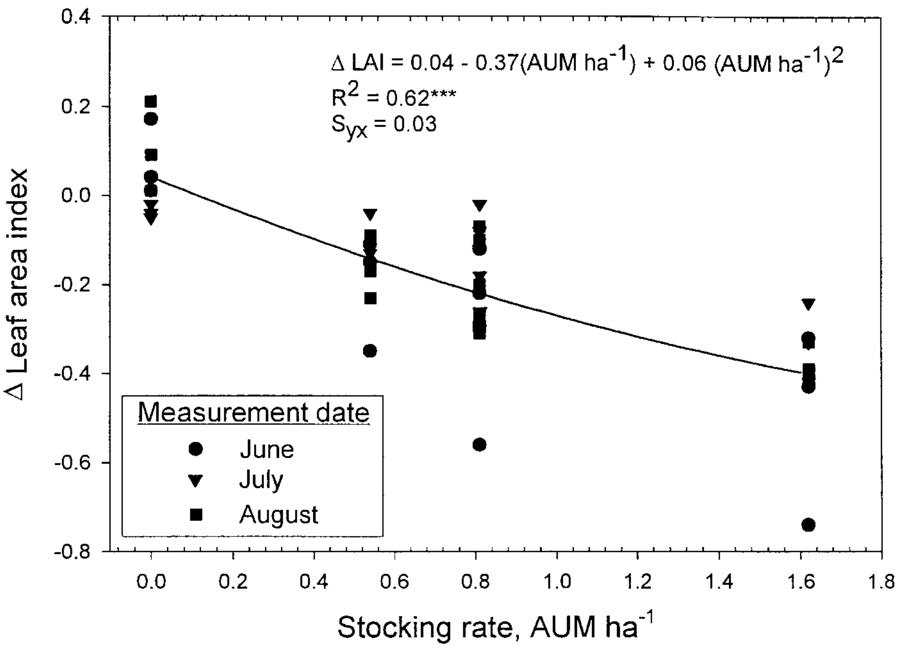

Fig. 3. Relationship between change in leaf area index following grazing versus stocking rate for Sandhills range. The regression equation was developed from measurements made mid-June (circle), mid-July (down triangle), and mid-August (square) 1991.

mean tilt angle (MTA) are useful in interpretation of physiological responses to various grazing strategies at the plant community level. This application could offer significant advantages in the study of grazing management and warrants further investigation in additional native grassland canopy types.

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Sagebrush response to ungulate browsing in Yellowstone

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Abstract

Big sagebrush (*Artemisia tridentata* Nutt.) declined from ungulate browsing during the first half of the twentieth century on the Northern Yellowstone Winter Range. It was our objective to compare shrub parameters of Northern Yellowstone Winter Range sagebrush habitat types continually browsed or protected for 32 to 37 years. Measurements were taken in and out of exclosures for 19 environmentally paired, protected, and browsed sites. We found significant differences in development between protected and browsed shrubs. Big sagebrush canopy cover at the 19 sites averaged 19.7% with protection and 6.5% where browsed ($P \leq 0.0027$), and plants were twice as numerous ($P \leq 0.0027$) under protection. Winter forage production of individual big sagebrush plants was also greater under protection at 16 of the 19 paired sites ($P \leq 0.0027$). Subdominant sprouting shrubs generally responded the same as big sagebrush. This ungulate induced decline of shrubs has implications for many Northern Yellowstone Winter Range values. Ultimately many organisms are sacrificed with the loss of quality big sagebrush habitat.

Key Words: *Artemisia tridentata*, big sagebrush, winter range, *Cervus elaphus*, elk, *Odocoileus hemionus*, mule deer, *Antilocapra americana*, pronghorn.

Resumen

En el "Northern Yellowstone Winter Range", el "Big sagebrush" (*Artemisa tridentata* Nutt) declinó durante la primera parte del siglo veinte debido al ramoneo por los ungulados. Nuestro objetivo fue comparar los parámentros de arbustos en tipos de hábitats de "sagebrush"en el "Northern Yellowstone Winter Range" y que han sido continuamente ramoneados o protegidos del ramoneo durante 32 a 37 años. Las mediciones fueron tomadas dentro y fuera de exclusiones en 19 sitios ambientalmente apareados con y sin ramoneo. Encontramos diferencias significativas en el desarrollo de arbustos ramoneados y protegidos. La cobertura de copa del "Big sagebrush" en los 19 sitios promedió 19.7% con protección y 6.5% cuando fueron ramoneadas ($P \leq 0.0027$) y el número de plantas fue el doble en las áreas protegidas ($P \leq 0.0027$). En 16 de los 19 sitios, la producción de forraje en invierno de plantas individuales de "Big sagebrush" también fue mayor cuando los arbustos estuvieron protegidos ($P \leq 0.0027$). Los arbustos rebrotantes subdominates generalmente respondieron de la misma manera que el "Big sagebrush". Esta reducción de arbustos inducida por los ungulados tiene implicaciones para muchos de los valores del "Northern Yellowstone Winter Range". Finalmente muchos organismos son sacrificados con la pérdida de calidad del hábitat del "Big sagebrush"

Since at least the 1920's, the effects of large populations of ungulates on the Northern Yellowstone Winter Range have been debated. Most attention has focused on the larger woody plants, primarily aspen (*Populus tremuloides* Michx.) and willows (*Salix* L.). Since adoption of the Natural Regulation Policy in 1968 in Yellowstone National Park there has been little concern for the decline of woody plants, especially sagebrush (*Artemisia* L.) taxa (Wambolt 1998). However, during the early twentieth century a good deal of concern was expressed for the welfare of sagebrush within Yellowstone National Park (Rush 1932, Wright and Thompson 1935, Cahalane 1943, Kittams 1950). In response, the National Park Service constructed 10 exclosures on the Northern Yellowstone Winter Range in 1957 and 1962, a period of high elk numbers, partially to study the relationships between ungulate foraging and sagebrush. Eight of these exclosures still exist, of which 4 are totally in sagebrush habitat types and all 8 contain a significant portion within a sagebrush habitat type. Recently, more attention has been given sagebrush taxa on the Northern Yellowstone Winter Range regarding their forage relationships with ungulates. Investigations have determined mechanisms unique to sagebrush taxa and the Northern Yellowstone Winter Range that influence sagebrush browsing patterns and heavy levels of use (Personius et al. 1987, Striby et al. 1987, Wambolt and McNeal 1987, Bray et al. 1991, Wambolt et al. 1994, Singer and Renkin 1995, Wambolt 1996). To refine our knowledge of sagebrush-herbivory relationships on the Northern Yellowstone Winter Range, it was our objective to compare parameters between shrubs ungulate browsed or protected since exclosure construction.

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Methods

Study Area

The Northern Yellowstone Winter Range occupies 100,000 ha over an 80 km stretch along the lower elevations in northern Yellowstone National Park and extends northward into Montana along the Yellowstone River drainage (Houston 1982). The Lamar and Gardiner rivers also drain portions of the lowlands in Yellowstone National Park that are relatively free of snow, thereby providing a reliable winter location for ungulate foraging (Houston 1982). Singer (1991) reported that 80% of the ungulates in Yellowstone National Park during winter are found on the Northern Yellowstone Winter Range. In addition, up to 2,544 Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) and 8,626 Rocky Mountain elk (*Cervus elaphus* nelsoni) have been counted during late winter on the portion of the Northern Yellowstone Winter Range north of the Yellowstone National Park boundary in Montana (Unpublished data, Montana Fish, Wildlife & Parks). Actual counts (no adjustment for sightability) of elk on the Northern Yellowstone Winter Range increased from an average of 4,382 animals during the 1962 to 1969 period (Houston 1982) (pre-Natural Regulation influence) to an average of 17,409 based on 9 counts between 1982 and 1995, after adoption of the Natural Regulation Policy (Unpublished data, Montana Fish, Wildlife & Parks).

The favorable climate for ungulate winter foraging varies across the Northern Yellowstone Winter Range. Coughenour (1991) reported 279 mm of annual precipitation at Gardiner, Montana (1,616 m), 398 mm at Mammoth (1,899 m), and 406 mm at Tower Falls (1,912 m). Within the portion of the Northern Yellowstone Winter Range used in this study, Gardiner is the lowest elevation studied, while some sites were 100–200 m higher than Tower Falls. Half of the precipitation is received as snow although peak moisture is received in spring and early summer (Farnes 1991). The soils at the study sites are typic calciborolls, aridic haploborolls, and aridic calciborolls (Lane 1990). The Gardiner area is located on ancient mudflows which are higher in clay and lower in fertility than the rest of the study area.

The habitat type in the Gardiner area is Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young)-bluebunch wheatgrass (*Agropyron spicatum* [Rydb.] Scribn.). Over the rest of the Northern Yellowstone Winter Range the mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle)-Idaho fescue (*Festuca idahoensis* Elmer)-bluebunch wheatgrass habitat type dominates. Important plants include the sprouting shrubs associated with sagebrush habitat types, specifically rubber rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), green rabbitbrush (*C. viscidiflorus* [Hook.] Nutt.) and gray horsebrush (*Tetradymia canescens* D.C.) which were found throughout the study area. Other important grasses were prairie junegrass (*Koeleria macrantha* Ledeb.), and Sandberg bluegrass (*Poa secunda* Presl.).

Pronghorn (*Antilocapra americana americana*), mule deer, and elk occupy the portion of the Northern Yellowstone Winter Range studied near Gardiner. Only elk forage on sagebrush in significant numbers during winter over the rest of the Northern Yellowstone Winter Range (Singer and Renkin 1995). During the last decade bison (*Bison bison bison*) have been observed near some of the exclosures, but there is no evidence that bison have had significant impact on the shrubs of sagebrush habitat types.

Sampling and Analysis

Sampling followed the general procedure detailed by Coughenour (1991). Because the large Yellowstone fires of 1988 burned the vegetation in 2 of the 8 remaining exclosures, measurements were taken in (protected) and near (browsed) the 6 unburned exclosures (Table 1). The 2 ha exclosures contained considerable environmental variation. Because important differences in shrub parameters could exist among various environmental conditions, the sagebrush habitat type within each exclosure was stratified to separate topographic, soil, and microclimatic variation (Coughenour 1991). Pairing sites with similar slopes and aspects accomplished this stratification. This resulted in 19 environmentally paired sites within and adjacent to the 6 exclosures. Coughenour (1991) emphasized that this stratification procedure is preferable to pure randomization in experiments of this nature to insure that biases are not allowed by inadvertent grouping of samples on a confounding environmental gradient (Hurlbert 1984). We agree with Coughenour (1991) that with random sampling using paired sites (in and out of the exclosures) it is unlikely that comparable distributions of topo-edaphic positions would have been obtained, regardless of sample size.

No sampling outside exclosures was done within 50 m of the fenceline to avoid a potential "exclosure effect" created by ungulates walking the perimeter fence. To further assure that we were not measuring an "exclosure effect", we also environmentally paired remote sites with 4 of the 19 original paired sites. The 4 remote browsed sites were located between 300 m and 450 m from the exclosures.

Data were collected during summer 1994. Canopy coverage and density of big sagebrush and sprouting shrubs were compared in and out of the exclosures. In addition, winter forage production was estimated for big sagebrush subspecies (Wambolt et al. 1994). At each of the 19 sites, ten, 30-m transects were located inside the exclosure and another

Table 1. Slopes and aspects at the 19 locations where browsed and protected sites were paired by both characters. The paired sites are associated with the 6 exclosures established either in 1957 or 1962 (Lamar-57 etc.) that were not burned during the Yellowstone fires of 1988.

Site[1]	Slope[2]	Aspect
Mammoth–57[3]	Gentle	NWW
Junction Butte–62A[3]	Moderate	SE
Junction Butte–62B	Gentle	N
Lamar–57A	Steep	SSW
Lamar–57B	Very steep	SW
Lamar–57C	Moderate	SW
Lamar–57D	Steep	SW
Lamar–62A	Steep	S
Lamar–62B	Very steep	S
Lamar–62C[3]	Moderate	S
Lamar–62D	Moderate	SW
Gardiner–57A	Flat	Flat
Gardiner–57B	Steep	E
Gardiner–57C	Gentle	SW
Gardiner–57D	Gentle	NWW
Gardiner–62A	Moderate	NEE
Gardiner–62B[3]	Flat	Flat
Gardiner–62C	Very steep	NEE
Gardiner–62D	Very steep	SE

[1]The 8 Gardiner sites are dominated by Wyoming big sagebrush and the other 11 sites by mountain big sagebrush.
[2]Slope classes are: Flat ≤3%, Gentle = 4–15%, Moderate = 16–29%, Steep = 30– 44%, Very steep ≥45%.
[3]At these locations a remote site was paired environmentally with the original protected and browsed pair.

10 transects outside the exclosure by stratifying the site so that each transect would represent an equal sized portion of the entire site. Along each 30-m transect, the line interception method (Canfield 1941) was used to obtain percent shrub canopy coverage. All shrub canopy segments of at least 3 cm were included. Along each 30-m line, belt transects of 2 x 30 m were created by measuring 1 m on both sides of the line transect. Densities of established shrubs were obtained within the 10 belt transects. Established shrubs were considered to be those having an average horizontal axis (canopy) ≥15 cm from 4 canopy measurements (Wambolt et al. 1994). All measurements were taken in a similar manner at the 4 remote locations.

Winter forage production of big sagebrush was estimated by using models developed on the Northern Yellowstone Winter Range for individual subspecies and browse form classes (Wambolt et al. 1994). These models will predict winter forage production (R^2 = 0.91–0.94) for plants with ≥15 cm average canopy. Specific measurements varied depending on taxon and browse form class (Wambolt et al. 1994). Ten plants for production measurements were selected in each belt transect by totaling the number of plants and dividing by 10, after which every plant of that multiple was measured. On the browsed portion of the 8 Gardiner paired sites, winter forage production of Wyoming big sagebrush could not be estimated because plants >15 cm average canopy were not located.

Exploratory data analysis indicated unequal variances from site to site. Consequently, 2-sample t procedures were used at each site and over all sites to test for differences in canopy coverage, density, and winter forage production between protected and browsed shrubs. To make simultaneous inferences at the P = 0.05 level, the tests were adjusted using the Bonferroni (Neter et al. 1996) procedure. This adjustment yielded an overall comparative P-value of 0.0027.

Results and Discussion

Since the period of exclosure construction in 1957 and 1962, there has been a significant difference in the development of protected and browsed big sagebrush communities (Fig. 1). Average big sagebrush canopy cover on protected sites (Table 2) was 202% greater (P≤0.0027) than on browsed sites over the 19 paired sites. The average big sagebrush cover for all 19 sites was 19.7% inside and 6.5% outside the exclosures. This relationship was universal on sites with Wyoming big sagebrush or mountain big sagebrush, flat to very steep topographies, and all aspects and precipitation levels.

Fig. 1. A Wyoming big sagebrush plant at the Gardiner–57 exclosure. The plant is growing with half of its crown inside the exclosure. The portion outside the exclosure is nearly dead from heavy browsing. Despite ungulates reaching through the fence, the inside half of the plant is much thriftier with a moderate amount of use.

The 8 study sites with Wyoming big sagebrush are in a locality that historically has been more heavily browsed than the portions of the Northern Yellowstone Winter Range with mountain big sagebrush (Houston 1982, Singer and Renkin 1995). This is logical as Wyoming big sagebrush favors the relatively dry environments that also offer the best winter foraging opportunities for ungulates. Partially due to both a lesser site potential and the long-term heavy browsing at the Wyoming big sagebrush sites, even with protection those 8 sites only averaged 7.8% cover compared to 28.4% for mountain big sagebrush at the 11 sites where it grows. The Wyoming big sagebrush sites under protection averaged 857% more sagebrush cover than where browsing has continued since 1957 and 1962. The same figure was also high for mountain big sagebrush at 166%.

We found that although all of the 19 sites did not have the same potential to support big sagebrush, the relationships were consistent throughout the range of conditions represented. Big sagebrush cover in the protected portions of the study sites ranged from 1.4 to 49.5% and in the browsed portions from 0 to 28.7%. The high cover (49.5%) at the Mammoth-57 site indicates a favorable environment for sagebrush. Historically, the site probably has endured less browsing than the other sites due to its NWW aspect and gentle slope that both reduce solar radiation effectiveness coupled with relatively high amounts of snow at Mammoth. This conclusion is logical when Mammoth-57 is compared to Lamar-57-C and Lamar-62-C and D sites that also had high amounts of sagebrush cover with protection inside the exclosure. These 3 sites collectively had 30% as much sagebrush cover on the outside as on the inside, while the same figure for Mammoth-57 was 58%. This was due at least partially to easier access for browsing ungulates with lesser snow accumulations on the Lamar sites resulting from steeper slopes on S to SW aspects. This combination greatly increases the effectiveness of solar radiation for melting snow (Trewartha 1968), thereby facilitating browsing.

Ungulate browsing also affected big sagebrush density. Big sagebrush plants

Table 2. **Percent canopy cover of big sagebrush at 19 environmentally paired sites either browsed or protected.**

Site	Protected	Browsed	Probability > t[1]
	----------- (%)	-----------	
Mammoth–57	49.5	28.7 (28.8)[2]	0.0004
Junction Butte–62A	31.9	11.6 (18.8)	0.0000
Junction Butte–62B	32.1	11.5	0.0001
Lamar–57A	3.2	0.1	0.0291
Lamar–57B	2.9	0.1	0.0002
Lama –57C	44.3	19.8	0.0004
Lamar–57D	25.4	16.9	0.0015
Lamar–62A	9.3	1.3	0.0005
Lamar–62B	29.6	8.2	0.0001
Lamar–62C	41.7	9.3 (9.0)	0.0004
Lamar–62D	42.1	9.7	0.0000
Gardiner–57A	3.9	0.0	0.0001
Gardiner–57B	3.6	0.1	0.0004
Gardiner–57C	4.5	1.1	0.0001
Gardiner–57D	1.4	0.4	0.0073
Gardiner–62A	21.8	0.4	0.0001
Gardiner–62B	17.6	4.3 (1.5)	0.0000
Gardiner–62C	2.4	0.2	0.0012
Gardiner–62D	6.8	0.0	0.0001

[1]The comparative P value for similar inferences is 0.0027.
[2]Numbers in parentheses in this column are the percent canopy cover of big sagebrush at a remote site that paired environmentally with the protected and browsed pair.

across the Northern Yellowstone Winter Range were twice as numerous with protection as with browsing (Table 3). The average density of big sagebrush plants was 30.5 per 60 m^2 inside and 15.3 per 60 m^2 outside the exclosures ($P \leq 0.0027$). Big sagebrush cover and density were highly associated ($r = 0.92$; $P \leq 0.000$) inside the exclosures with protection and also outside where browsing occurred ($r = 0.93$; $P \leq 0.000$). Although the correlations are strong, there were some situations where a relatively large number of small sagebrush plants were found. These aggregations were in openings in the sagebrush canopy created where the predecessor plants had been overbrowsed, allowing seedlings to establish. Although snow cover is relatively light throughout the Northern Yellowstone Winter Range, some snow falls each winter and may protect the small plants for several years before they are available for ungulate foraging. Hoffman (1996) working in the Gardiner basin of the Northern Yellowstone Winter Range found that 47% of all the mountain big sagebrush plants that established during the 1978–1992 period, established during 1988. That year offered relatively good seed production due to plentiful spring moisture followed by a winter with considerably more snow than prevailed through the 15 year period (Hoffman 1996). These conditions were coupled with a great reduction in elk (Montana Fish, Wildlife & Parks and Yellowstone National Park unpublished data) due to the most severe winter of the period in 1988-1989, and some loss of forage from the large 1988 Yellowstone fires.

Individual mountain big sagebrush plants produced 88% more winter forage where protected ($P \leq 0.0027$) (Table 4). Only the 11 sites with mountain big sagebrush were included in Table 4, as browsed portions of all 8 Wyoming big sagebrush sites contained only sagebrush plants that were too small (≤15 cm average canopy) for production to be estimated by the model (Wambolt et al. 1994). Therefore, of the 19 protected sites, all 8 Wyoming big sagebrush sites plus 8 of the 11 mountain big sagebrush sites produced significantly ($P \leq 0.0027$) more winter forage on a per-plant basis than the browsed portions of the site. Big sagebrush winter forage production can be converted to a unit area basis when used with density. Because the density of protected plants was also significantly greater ($P \leq 0.0027$) than for browsed plants at 15 sites, considerably more big sagebrush winter forage was produced per unit area on protected sites.

Sprouting shrubs (rubber rabbitbrush, green rabbitbrush, and gray horsebrush), comprised much less canopy cover than did big sagebrush (Table 5). The sprouting shrubs collectively averaged 2% cover in the protected areas and 1.1% in the paired browsed locations ($P \leq 0.0027$). The relationship of more sprouting shrub cover on the protected sites was not consistent at all locations. However, 12 of the 19 sites did have more sprouting shrub cover measured on the protected portion of the site, but the difference in this character was only significant at 3 locations.

Density of sprouting shrubs averaged 16.6 per 60 m^2 where protected, compared to 13.1 per 60 m^2 on the browsed

Table 3. **Number of big sagebrush plants (with a minimum canopy of 15 cm) per 60 m^2 at 19 environmentally paired sites either browsed or protected.**

Site	Protected	Browsed	Probability > t[1]
	----------- (No.)	-----------	
Mammoth–57	51.6	51.5 (53.6)[2]	0.9843
Junction Butte– 62A	51.3	24.3 (24.9)	0.0001
Junction Butte–62B	54.9	33.4	0.0000
Lamar–57A	2.3	0.4	0.0022
Lamar–57B	7.9	0.0	0.0001
Lamar–57C	56.7	37.2	0.0000
Lamar–57D	46.0	42.9	0.4202
Lamar–62A	34.0	7.0	0.0006
Lamar–62B	53.0	37.3	0.0018
Lamar–62C	52.4	18.4 (18.3)	0.0000
Lamar–62D	45.6	29.7	0.0046
Gardiner–57A	9.0	0.5	0.0002
Gardiner–57B	8.1	0.5	0.0002
Gardiner–57C	15.1	5.0	0.0005
Gardiner–57D	7.7	1.0	0.0001
Gardiner–62A	36.0	1.2	0.0001
Gardiner–62B	39.2	0.2 (1.6)	0.0001
Gardiner–62C	2.2	0.0	0.0090
Gardiner–62D	6.9	0.7	0.0001

[1]The comparative P value for similar inferences is 0.0027.
[2]Numbers in parentheses in this column are the number of big sagebrush plants at a remote site that paired environmentally with the protected and browsed pair.

portions of the 19 sites. For 4 of the 19 paired locations the differences between their values were statistically significant, 3 of which had more individuals on the protected portion (Table 6).

In general, response of the sprouting shrubs was similar to that of big sagebrush over the Northern Yellowstone Winter Range. Not surprisingly, the degree of response to browsing and protection was considerably less for the sprouting shrubs than for the non-sprouting big sagebrush. Sprouters often initially thrive with disturbance like heavy browsing as they sustain prolonged herbivory better than non-sprouters. The taxa we measured are known to often benefit when associated species are preferred forages and over-utilized (Young and Evans 1978, Blaisdell et al. 1982). On the Northern Yellowstone Winter Range the dominant big sagebrush has been reduced from intense browsing, thereby providing the subdominant sprouting shrubs an opportunity to increase. Although no production data were obtained for our sprouting shrubs, it is obvious that the biomass produced by these plants is small on the Northern Yellowstone Winter Range, despite the inherent resiliency of sprouting shrubs to browsing. Apparently even the sprouting shrubs have been retarded by Northern Yellowstone Winter Range browsing over the long-term ($P \leq 0.0027$).

The 4 remote sites that we matched with specific paired sites assured us that we were not biasing our results by measuring an "exclosure effect" created when ungulates might forage heavily along exclosure perimeters. All of the t-values found comparing the 4 remote locations and the paired 4 protected sites arrived at the same conclusions for the 5 parameters in Tables 2–6.

Pronghorn and mule deer often forage heavily on big sagebrush taxa (Welch and McArthur 1979). Mule deer diets averaged 52% big sagebrush over a 10 year period (Wambolt 1996) only a couple km away from the 8 Wyoming big sagebrush sites. A high degree of utilization is reflected in the great impact on Wyoming big sagebrush populations at these 8 sites where elk may also be present with pronghorn and mule deer (Singer and Renkin 1995). However, as Singer and Renkin (1995) point out, elk are the only significant browsers at the other 11 sites due to excessive snow depths. Therefore, with our findings, it becomes obvious that elk numbers were large enough on the Northern Yellowstone Winter Range for a sufficient number of years before exclosure construction started in 1957 to greatly reduce big sagebrush populations (Rush 1932, Wright and Thompson 1935, Cahalane 1943, Kittams 1950).

Mountain big sagebrush on the Northern Yellowstone Winter Range was preferred over Wyoming big sagebrush by mule deer and elk (Wambolt 1996). The fact Wyoming big sagebrush in this study is impacted from browsing even more than mountain big sagebrush is therefore, a function of snow depth limiting pronghorn and mule deer foraging instead of a foraging preference for Wyoming big sagebrush. The crude terpenoids present in 4 sagebrush taxa on the Northern Yellowstone Winter Range explained why ungulates displayed a preference (Personius et al. 1987, Bray et al. 1991). However, a 10 year data set made it clear that any of the sagebrush taxa on the Northern Yellowstone Winter Range would be heavily browsed if winter conditions precluded ungulates from exercising their preferences (Wambolt 1996).

Other studies conducted at Northern Yellowstone Winter Range exclosures have concluded that ungulate foraging

Table 4. Average grams of winter forage produced per mountain big sagebrush plant at 11 environmentally paired sites either browsed or protected. The 8 Gardiner area Wyoming big sagebrush sites are not included because browsed plants at those sites were too severely impacted by browsing to meet the minimum size requirements to model production. This obviously resulted in significantly less production where browsed at each of those 8 sites.

Site	Protected	Browsed	Probability > t[1]
	----------- (g)	-----------	
Mammoth–57	184.5	99.9 (113.5)[2]	0.0000
Junction Butte–62A	161.3	88.0 (90.3)	0.0000
Junction Butte–62B	200.1	92.1	0.0001
Lamar–57A	86.0	21.5	0.0039
Lamar–57B	93.7	0.0	0.0001
Lamar–57C	222.5	133.1	0.0003
Lamar–57D	120.8	108.7	0.2069
Lamar–62A	96.2	70.2	0.0001
Lamar–62B	141.0	83.3	0.0126
Lamar–62C	122.5	80.6 (99.7)	0.0023
Lamar–62D	188.0	81.3	0.0000

[1]The comparative P value for similar inferences is 0.0027.
[2]Numbers in parentheses in this column are winter forage produced per big sagebrush plant at a remote site that paired environmentally with the protected and browsed pair.

Table 5. Percent canopy cover of all sprouting shrubs at 19 environmentally paired sites either browsed or protected.

Site	Protected	Browsed	Probability > t[1]
	----------- (%)	-----------	
Mammoth–57	1.9	2.5 (2.4)[2]	0.5452
Junction Butte–62A	0.3	0.5 (1.2)	0.3336
Junction Butte–62B	6.7	3.9	0.0464
Lamar–57A	4.6	2.1	0.0128
Lamar–57B	2.7	3.0	0.6975
Lamar–57C	0.1	0.3	0.2660
Lamar–57D	1.6	0.6	0.1172
Lamar–62A	6.1	0.8	0.0106
Lamar–62B	1.5	3.2	0.0028
Lamar–62C	0.3	0.3 (0.5)	0.9196
Lamar–62D	0.0	0.0	
Gardiner–57A	1.9	0.6	0.0089
Gardiner–57B	2.3	1.3	0.0367
Gardiner–57C	2.0	1.1	0.0226
Gardiner–57D	2.7	0.9	0.0007
Gardiner–62A	1.0	0.2	0.0002
Gardiner–62B	0.1	0.0(0.4)	0.0223
Gardiner–62C	1.9	0.3	0.0000
Gardiner–62D	0.8	0.1	0.0146

[1]The comparative P value for similar inferences is 0.0027.
[2]Numbers in parentheses in this column are percent canopy cover of sprouting shrubs at a remote site that paired environmentally with the protected and browsed site.

Table 6. Number of sprouting shrubs per 60 m2 at 19 environmentally paired sites either browsed or protected.

Site	Protected	Browsed	Probability > t[1]
	---------- (No.)	----------	
Mammoth–57	29.0	33.4 (34.8)[2]	0.5404
Junction Butte–62A	5.1	12.6 (18.3)	0.0054
Junction Butte–62B	60.3	81.6	0.0021
Lamar–57A	34.4	18.0	0.0126
Lamar–57B	22.0	7.8	0.0000
Lamar–57C	5.3	6.5	0.4155
Lamar–57D	18.6	8.5	0.0546
Lamar–62A	47.4	5.9	0.0001
Lamar–62B	19.7	30.3	0.0063
Lamar–62C	9.5	5.0 (7.4)	0.0484
Lamar–62D	8.3	8.2	0.9980
Gardiner–57A	8.8	6.6	0.2169
Gardiner–57B	10.9	6.5	0.0660
Gardiner–57C	7.4	5.7	0.3810
Gardiner–57D	3.1	7.6	0.0117
Gardiner–62A	22.3	3.3	0.0019
Gardiner–62B	0.1	0.0 (4.8)	0.3434
Gardiner–62C	1.8	1.7	0.8944
Gardiner–62D	1.0	0.4	0.2011

[1]The comparative P value for similar inferences is 0.0027.
[2]Numbers in parentheses in this column are the number of sprouting shrubs at a remote site that paired environmentally with the protected and browsed pair.

has had little effect on the vegetation (Coughenour 1991, Singer and Renkin 1995). Singer and Renkin (1995) reported that ungulates had suppressed Wyoming big sagebrush on the lower elevations of the Northern Yellowstone Winter Range, but had not affected the preferred mountain big sagebrush (Wambolt 1996), the dominant on 97% of the Northern Yellowstone Winter Range sagebrush habitat types. Singer and Renkin (1995) relied on data obtained from single paired belt transects (1.5 m x 30.5 m) established when the exclosures were constructed. These transects sampled <8% of the area included in our belt transects for the first 5 years of their data. Singer and Renkin (1995) obtained additional information in 1986 and 1987 by sampling a total of 140 m^2 (23% of our sampled area) in 15 randomly located 9.3 m^2 circular plots both inside and outside 6 exclosures. We conclude that our results differ from Singer and Renkin (1995) due to their smaller sample in combination with their random placement of the plots. We agree with Coughenour (1991), as discussed earlier, that randomization is not desirable in such situations.

Coughenour (1991) studied responses of herbaceous vegetation at 4 of the Northern Yellowstone Winter Range exclosures. His conclusions were that elk winter grazing generally did not reduce productivity of herbaceous plants and that because root biomass of herbs was not affected by grazing that there was no net consequence of winter grazing on the herbs. Because we studied browse, our results are not contradictory. However, if no differences between inside and outside these exclosures are found, it is possible that the approximately 50 years of intense herbivory prior to exclosure construction produced a long-term effect that persists to the present inside the exclosure. Thus, finding no difference does not necessarily mean that recent herbivory has no impact. However, if studies like ours document differences at these sites, it can be assumed that the changes are due to protection from herbivory. It is clear that we did not simply measure shrub decline outside the exclosures compared to a climatically determined historical level inside each exclosure. We measured changes in big sagebrush parameters since exclosure construction in 1957 and 1962. We do not have assurance that the recovery inside exclosures is complete.

Singer and Renkin (1995) concluded that the 66% decline in mule deer using the lower elevation within the Northern Yellowstone Winter Range over the previous 2 decades may be due to the decline in Wyoming big sagebrush. We concur and believe the decline we found across the Northern Yellowstone Winter Range in both Wyoming and mountain big sagebrushes negatively impacts each of the ungulates that forage on these taxa. The value of big sagebrush as a highly digestible and nutritious forage is well established (Welch and McArthur 1979). Other Northern Yellowstone Winter Range values would be similarly affected with the demise of the natural dominant vegetation (Wambolt 1998). This decline of habitat value in the extensive big sagebrush habitat types of the Northern Yellowstone Winter Range will extend well beyond ungulates to reduce many native organisms (Welch 1997). To arrest this trend, ungulate numbers, especially elk, would have to be reduced. At present such action would conflict with the Yellowstone National Park policy of Natural Regulation.

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Botanical composition of cattle and vizcacha diets in central Argentina

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Abstract

Cattle (*Bos taurus*) and vizcacha (*Lagostomus maximus*) diets were examined monthly in the semiarid Caldenal in central Argentina. Cow-calf operations are the most important economic activities within the region. In spite of a widespread distribution of the vizcacha in Argentina, comparative studies of the diet of cattle and vizcacha are scarce. The objective of this work was to analyze the botanical composition, seasonal trends, and possible dietary overlap between cattle and vizcacha. Diets were determined by microscopic analysis of cattle and vizcacha feces collected from November 1994 through December 1995 in a shrubland community of the southern Caldenal. Grasses were the bulk of the diet for both herbivores. *Piptochaetium napostaense* (Speg.) Hack. was the most abundant grass in vizcacha (53%) and cattle (40%) diets. *Prosopis Caldenia* Burk. pods partially (34%) replaced this grass in cattle diets during late summer and fall. Consumption of *P. napostaense* was generally higher (13%) in vizcachas than in cattle, especially during the dry period of the study (21%). During the drier months, cattle consumed more of the less preferred grasses (48%). Forbs were poorly represented in the diets perhaps because of scarce rains and low availability. Classification and ordination techniques revealed seasonal trends and overlapping diets. A greater overlap (75%) was found during the wet period due to simultaneous consumption of *P. napostaense* by both herbivores. Trends in diet diversity were similar with indices generally higher for cattle than for vizcachas, especially during the dry period.

Key Words: free ranging cattle, diet composition, semiarid area, microhistology.

Resumen

Las dietas de vacunos (*Bos taurus*) y vizcachas (*Lagostomus maximus*) fueron examinadas mensualmente en el Caldenal semiárido del centro de Argentina. La ganadería es la principal actividad en la región. A pesar que la vizcacha se encuentra ampliamente distribuida en la Argentina, existen pocos estudios comparativos de la dieta de vacunos y vizcachas. El objetivo de este trabajo fue analizar la composición botánica, tendencias estacionales y posible superposición dietaria entre vacunos y vizcachas. Las dietas se determinaron por análisis microhistológico de heces de vacunos y vizcachas recogidas desde noviembre de 1994 hasta diciembre de 1995 en una comunidad arbustiva del sur del Caldenal. Las gramíneas fueron el principal componente de la dieta de ambos herbívoros. *Piptochaetium napostaense* (Speg.) Hack fue la gramínea más abundante en las dietas de vizcachas (53 %) y vacunos (40 %). Los frutos de *Prosopis caldenia* Burk. reemplazaron parcialmente (34%) a esta gramínea en la dieta de vacunos durante el verano tardío y otoño. Las vizcachas generalmente consumieron más *Piptochaetium napostaense* (13 %) que los vacunos, especialmente durante el período seco del estudio (21%). Durante los meses más secos los vacunos consumieron gramíneas menos preferidas (48 %). Las dicotiledóneas herbáceas fueron escasas en la dieta de ambos herbívoros, quizás por la baja disponibilidad debida a las escasas lluvias. Las técnicas de clasificación y ordenamiento revelaron las tendencias estacionales y la superposición de dietas. Una gran superposición de dietas (75%) se encontró durante el período húmedo del estudio debido a que ambos herbívoros consumieron principalmente *Piptochaetium napostaense*. Las tendencias en la diversidad dietaria fueron similares con índices generalmente más altos para el ganado que para las vizcachas, especialmente durante el período seco.

Wild and domestic herbivores directly influence plant communities with their selective grazing. Floristic changes are highly variable and depend on many factors such as preferences of herbivores, the relative abundance and availability of forages, season of the year, and temporal and spatial overlap when more than one species grazes the same area.

The Southern Espinal (Fernández et al. 1989) or District of the Caldén (Cabrera 1976), commonly referred to as the Caldenal, is a temperate semiarid region in central Argentina characterized by the presence of *Prosopis caldenia* Burk. The landscape in the southern Caldenal is dominated by shrub-

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lands with a very rich grass layer. Poor range management is common throughout the region, and soil erosion and plant community deterioration are incipient but generalized (Fernández et al. 1989, Bóo and Peláez 1991).

The plains vizcacha (*Lagostomus maximus*, Chinchillidae) is a native rodent of Paraguay, Bolivia, and Argentina that inhabits grasslands and scrub (Branch and Sosa 1994). It is abundant in the Southern Caldenal and has been considered a plague in Argentina since 1907 because of its burrowing and foraging habits. Adult females (2.9–3.3 kg), adult males (4.5–5.6 kg) and young individuals live in groups of 9 to 14 individuals per colony (Branch et al. 1993). Daily intake by adults is 1.7–4.7% of body weight (Jackson 1985), and areas around the vizcacha colonies are characterized by bare soil with scarce, low-growing forbs and grasses.

Studies of the diet of cattle and vizcacha in semiarid Argentina are very scarce. Giulietti and Jackson (1986) studied food habits of vizcacha and cattle and found little similarity in their diets. They concluded that potential competition was low between both herbivores, but knowledge of the botanical composition of vizcacha and cattle diets where both herbivores graze a common area is much needed. The objective of this work was to analyze the botanical composition, seasonal variation, and dietary overlap of cattle and vizcacha diets in a plant community typical of the southern Caldenal.

Study Area and Methods

Cano et al. (1980) have described the vegetation of La Pampa where most of the Caldenal occurs. The study was conducted in a 600 ha pasture located in southeast La Pampa (Argentina) at 38°45'S, 63°45'W with mean elevation of 80 m. Mean annual rainfall is 448 mm with about 60% occurring in spring and fall. Mean annual potential evapotranspiration is 800 mm (Peláez 1986), and the mean annual temperature is 15.3°C with a minimum mean of 7°C (July) and a maximum mean of 23.6°C (January). Recorded maximum and minimum temperatures are 42.5°C and –12.8°C respectively. Soil at the study site is a Calciustoll with a petrocalcic horizon at an average depth of 0.60 m (Fernández et al. 1989).

The research area supports a plant community defined as "Unidad C" by Bóo and Peláez (1991). This community is characterized by a woody species cover of 50–70 % with *Prosopis caldenia* Burk., *P. flexuosa* D. C. and *Condalia microphylla* Cav. as the most abundant. The herbaceous cover is about 40–50% with *Piptochaetium napostaense* (Speg.) Hack. and *Stipa tenuis* Phil. as the major grasses. *Stipa speciosa* Trin. et Rupr. and *S. gynerioides* Phil. are frequent, and *S. clarazii* Phil., *Poa ligularis* Nees and *Pappophorum mucronulatum* Nees are scarce. *P. napostaense* and *S. tenuis* are good forage species that replace *Stipa clarazii* Phil and *Poa ligularis* Nees under moderate continuous grazing (Distel and Bóo 1995). Bare ground (30–40 %) is colonized during wet years by annual forbs, mostly *Medicago minima* (L.) Grufberg and *Erodium cicutarium* L'Herit. Annual above ground net primary production in this plant community for S. tenuis was 862 kg ha^{-1}, and 684 kg ha^{-1} for *P. napostaense* in a year with 532 mm of rainfall (Distel and Fernández 1986, Distel 1987).

Fifteen independent fecal samples from different mature cows were collected monthly from November 1994 to December 1995. These samples were analyzed following Bóo et al. (1991) to obtain 20% (P<0.05) precision in the estimation of the mean for species exceeding 6% of the total sample. On each sampling date, fresh fecal pellets from 10 vizcacha colonies were collected and analyzed in the same way. This sampling intensity gave a 20% (P<0.05) precision for species making up at least 4% of the sample (Bontti et al. 1995). Composition of cattle and vizcacha diets was determined by microscopic analysis of fecal samples (Sparks and Malechek 1968). Five slides were prepared from each sample and 40 microscope fields per slide were systematically viewed using 100X magnification. Fragments were identified by comparing fecal material with a reference collection that included most of the forages present in the area (Lindström 1994). Epidermal fragments were identified to species level except for *Ephedra* spp. and a few grasses and forbs. Differences between cattle and vizcacha diet components were analyzed using Student's t test (Ho: the relative composition of dietary components were equal in vizcacha and cattle feces; n = 10 for vizcacha and n = 15 for cattle).

Vegetation cover was visually estimated with the Braun-Blanquet (1979) abundance-cover scale in March 1995 (late summer), August 1995 (winter), and December 1995 (late spring), and we compared diet composition and forage abundance for those months. Cover estimation permits a rapid and nondestructive measure of food abundance, and estimates were made in and out of vizcacha colonies to detect possible differences in community composition. Plant taxa were grouped in 4 classes: woody species, forbs, preferred grasses and non-preferred grasses. This grouping was made because of the difficulty of identifying some taxa to species level especially during the winter when vegetative forms of grasses are similar. However, it was important to differentiate preferred and non-preferred grasses because diets may be correlated with forage availability. The woody species group included *Prosopis caldenia*, *Prosopis flexuosa*, *Condalia microphylla* and *Ephedra* spp. The forb group included *Erodium cicutarium* and *Medicago minima*. The preferred grasses included *Piptochaetium napostaense*, *Stipa tenuis*, *Pappophorum mucronulatum*, *Poa ligularis* and *Stipa clarazii*. The non-preferred grasses included *Stipa speciosa*, *Stipa gynerioides*, *Stipa trichotoma* and *Stipa tenuissima*. Student's t test was used to detect possible differences in botanical composition of the pasture in and out of vizcacha colonies (Ho: plant community composition was identical in and outside of vizcacha colonies; n = 10 on each site).

A matrix of the Bray and Curtis (1957) similarity index (BC_{jk}) between all possible pairs of average monthly diets was classified using complete linkage (Sneath and Sokal 1973, McInnis et al. 1990, Bóo et al. 1993). A possible distortion produced by the classification procedure was evaluated by the calculation of the cophenetic correlation coefficient (r_{xy}) following McInnis et al. (1990), and by ordination of the data matrix (DECORANA, Hill 1979).

Rainfall and temperature data were obtained locally with an automatic Zeeman station. Monthly diversity of cattle and vizcacha diets (N_2) were calculated as the reciprocal of Simpson's index (Hill 1973). Regression analyses using monthly rainfall and mean temperatures on monthly diet diversity for both herbivores were performed.

Results

Cattle diets.

During the study, rains were scarce (388 mm) and erratic, with a relatively wet period during the first 6 months followed by a pronounced drought and rain near the end of the study in November 1995 (Fig.1). Grasses dominated the diets of both herbivores throughout the study. However, diets varied among months and between herbivores within the same month.

Cattle relied heavily on *Piptochaetium napostaense*, one of the dominant perennial cool-season grasses on the study site, throughout the study (Fig. 2A). Monthly diet composition of this grass exceeded 65% during the first 3 months of the study. From February to July diet composition still exceeded 35%, but *P. napostaense* was partially replaced by *Prosopis caldenia* pods (Fig. 2G). For the rest of the study, *P. napostaense* made up less than 15% of the cattle diets, and it was basically replaced by 3 other grasses: *Stipa speciosa* (Fig. 2C), *S. gynerioides* (Fig. 2E) and *S. trichotoma* (Fig. 2D). These 3 grasses have been given low palatability rankings for cattle by Cano (1988), Bóo and Peláez (1991), and Distel and Bóo (1995). *Stipa tenuis* (Fig. 2B), a high yielding cool season grass (Distel and Fernández 1986), was present in low proportions in the diets with a maximum of 16% in July 1995. Forbs were scarce in cattle diets, and they reached a maximum of 7% in September. *Medicago minima* was the only forb in cattle diets in appreciable amounts (Fig. 2F). *Prosopis caldenia* pods consistently appeared in cattle diets (Fig. 2G). They were abundant from February through May (>30%) with a maximum of 40.5% in February. Other woody plants such as *Condalia microphylla* (Fig. 2H) and *Prosopis flexuosa* were very scarce in the cattle diets.

Vizcacha diets.

Grasses made up the majority of vizcacha diets throughout the study. *P. napostaense* contributed more than 64% of the vizcacha diets from November 1994 through May 1995. From June to August vizcacha consumption of *P. napostaense* declined and vizcacha consumed more *S. speciosa*, *C. microphylla* and *M. minima*. Vizcacha consumption of *S. tenuis* showed the lowest seasonal variation of all dietary components, and it was second to *P. napostaense* as the most important component of the vizcacha's diet. Vizcacha consumption of *S. tenuis* peaked at 26% in November 1995 but still ranked below *P. napostaense*. Other grasses such as *Stipa tenuissima* contributed less than 1% to vizcacha diets.

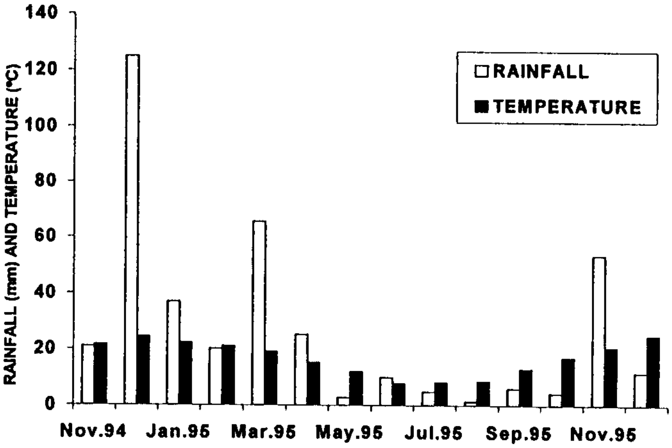

Fig. 1. Monthly rainfall and monthly averages of daily temperatures from November 1994 through December 1995 in a 600 ha. pasture in southeast La Pampa, Argentina.

Forbs made a maximum contribution (16%) to vizcacha diets in August 1995. *M. minima* was the most abundant forb in their diet. Because *M. minima* was not detected growing in the field during our study, we assumed the fruit fragments detected in their feces were produced in a previous growing season.

Woody plants were generally scarce in vizcacha diets. The most prominent was *C. microphylla* (23% in August 1995), and it was detected from June to December 1995. *P. caldenia* was not detected in vizcacha diets, and *P. flexuosa* contributed only trace amounts.

Comparisons of cattle and vizcacha diets.

There were marked similarities and differences among the principal dietary components of both herbivores (Fig. 2). In December 1994 cattle consumed more ($p<0.05$) *P. napostaense* than vizcachas. Equal proportions of *P. napostaense* occurred in the diets of both species in November 1994, and January and August 1995. For the rest of the study, vizcachas consistently consumed more *P. napostaense* than cattle. Vizcachas consumed more ($p<0.05$) *S.*

Table 1. Mean (n = 10) botanical composition ($\overline{X} \pm SE$) of the pasture by selected plant groups and mean (n = 10 for vizcacha; n = 15 for cattle) botanical composition ($\overline{X} \pm SE$) of cattle and vizcacha diet in March, August and December 1995 in Southeast La Pampa, Argentina.

Month	Pasture and diet composition				
	Preferred grasses	Non preferred grasses	Forbs	Woody species	Bare soil
	(%)				
March					
Pasture composition	32.6 ± 3.0	19.9 ± 3.5	2.9 ± 0.7	27.6 ± 3.8	15.7 ± 2.6
Cattle diet	64.1 ± 3.3	0.7 ± 0.2	0.7 ± 0.2	33.9 ± 3.2	—
Vizcacha diet	91.6 ± 1.7	0.7 ± 0.4	5.0 ± 1.5	0.3 ± 0.2	—
August					—
Pasture composition	27.4 ± 2.6	25.3 ± 2.9	1.1 ± 0.3	34.7 ± 5.5	16.5 ± 2.7
Cattle diet	20.4 ± 2.1	54.9 ± 1.7	6.5 ± 0.9	8.3 ± 1.1	—
Vizcacha diet	30.9 ± 2.7	23.4 ± 2.1	9.9 ± 2.6	24.1 ± 2.3	—
December					—
Pasture composition	24.0 ± 2.5	22.9 ± 2.3	1.1 ± 0.2	29.2 ± 3.3	17.7 ± 1.6
Cattle diet	19.6 ± 3.5	56.8 ± 2.9	4.0 ± 0.7	1.9 ± 0.4	—
Vizcacha diet	62.3 ± 2.7	13.4 ± 1.2	6.3 ± 1.1	2.2 ± 0.5	—

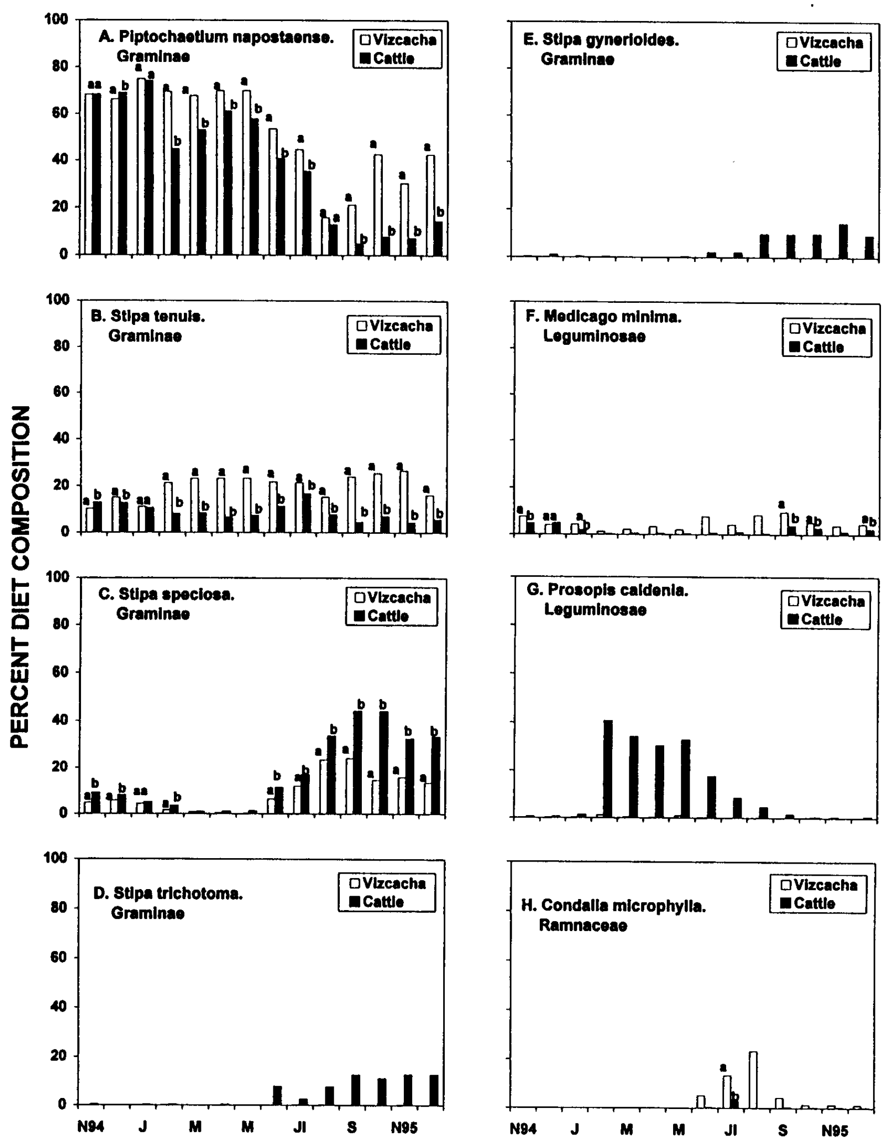

Fig. 2. Mean monthly contribution (percent) of forages contributing at least 8% to the total diet of vizcacha and cattle in central Argentina from November 1994 to December 1995. Paired bars sharing a common letter are not significantly different. (p>0.05).

tenuis than cattle during most of the study. Exceptions were November 1994, when cattle consumed more *S. tenuis* than vizcachas, and January 1995 when dietary proportions were equal. In most months when *Stipa speciosa* was found in cattle and vizcacha diets, its contribution was higher for cattle than vizcachas. During March, April, and May, *Stipa speciosa* was a trace component of both herbivore diets. Other grasses such as *S. Gynerioides* and *S. trichotoma* were detected in moderate (14%) to low (2%) amounts in the diets of cattle from June to December 1995.

Fruits of *M. minima*, the only appreciable forb in the diets, were generally more abundant in vizcacha than in cattle diets. Among the woody plants, *P. caldenia* pods were found only in cattle diets. Leaves of *C. microphylla* were found from June to December 1995 in vizcacha diets and in cattle diets only in July 1995.

Plant community composition.

Although we suspected there were differences in plant community composition within and adjacent to vizcachas colonies, our analyses did not support that hypothesis and the data were pooled. Table 1 summarizes those data and includes cattle and vizcachas diet composition data for the same periods.

Cluster analysis.

Seventeen of 19 taxa were present in both herbivore diets, indicating in qualitative terms, a high degree of dietary overlap. However, there were significant differences ($p<0.05$) in the proportions of components that appeared in the diet of each herbivore. Seasonal differences also occurred. These differences are evident from the groupings generated by the cluster analyses (Fig. 3). By cutting the tree in the range $62<BC_{jk}<63$ six groups were formed.

Cluster A included vizcacha diets from August, September, and November 1995. This 3-month period coincided with the minimum use of *P. napostaense* (Fig. 2A) and high use of *S. speciosa* (Fig. 2C) by vizcachas. This group is rather heterogeneous which is evidenced by its height. If we chose 74 instead of 63 as the upper limit of the BC_{jk} interval, the August 1995 vizcachas diet would be segregated as an "outlier" (sensu Gauch 1982). August 1995 was the month with the highest consumption of *C. microphylla* by vizcachas (Fig. 2H).

Cluster B groups cattle diets from August through December 1995 (mid winter and spring). During this period cattle consumed the lowest proportion of *P. napostaense* and *S. tenuis* (Fig. 2A,B) and relied more heavily on non-preferred grasses (*S. speciosa, S. trichotoma*, and *S. gynerioides*, Fig. 2C, D, E).

Cluster C was the largest and exhibited 2 well-defined subclusters. The first subcluster, contains the greatest overlap between the diets of both herbivores, and it encompasses the mid spring to mid summer (November and December 1994 and January 1995) diets of cattle and vizcachas. This period contained the greatest consumption of *P. napostaense,* moderate intake of *S. tenuis,* and low intakes of *S. speciosa* and *M. minima* (Fig. 2F). The second subcluster contains the mid summer to mid fall (February, March, April, and May 1995) diets of vizcachas which consisted almost entirely of *P. napostaense* and *S. tenuis.* Cattle diets were segregated from this subcluster into cluster F probably because of the high intake of *Prosopis*

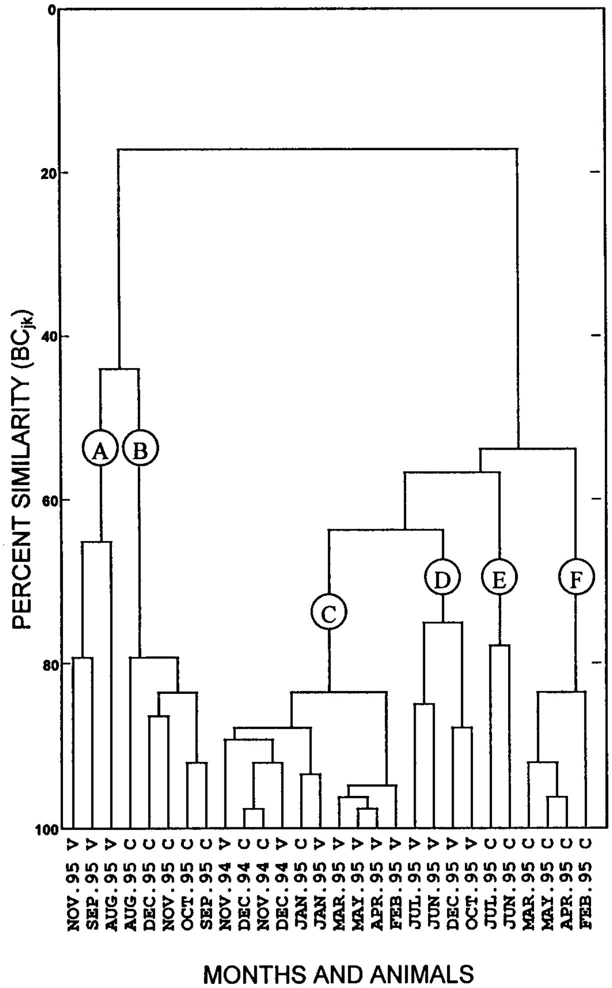

Fig. 3. Dendrogram of cluster analyses of monthly diets of vizcacha (VIZ) and cattle (CAT). A, B, C, D, E and F indicate defined clusters.

caldenia pods.

Cluster D contains the diets of vizcacha from June, July, October and December 1995. The main difference between cluster D and cluster A is a higher proportion of *P. napostaense* and a lower proportion of *S. speciosa* in D.

Cluster E, which is the smallest group, includes only the June and July diets of cattle. Based on the main diet components (Fig. 2) it is similar to cluster B but had a greater proportion of *P. napostaense* and *S. tenuis*, and a lower proportion of non-preferred grasses.

The cophenetic correlation coefficient, an index of possible distortion between the resemblance matrix and the classification procedure, was found to be $r_{x,y}$ = 0.86 which is considered acceptable. Values of $r_{x,y} \geq 0.80$ indicate that distortion is not great (McInnis et al. 1990).

Ordination output

Ordination output is shown in Figure 4. The first 2 axes (DC1 and DC2) had eigenvalues of 0.48 and 0.05 respectively. The different clusters generated by the classification are also depicted in Figure 4. The samples span a range of 250 units on the first axis indicating a high degree of homogeneity in the data. Two samples separated by 400 would have no species in common. This analysis suggested considerable overlap occurred for the entire study period.

Cluster B, C, and F were homogeneous and well separated on the first axis, whereas Clusters A, D and E were less homogeneous and did not show clear separation. The diets of cattle had a wider distribution on the axes than vizcacha diets. Cluster F, characterized by high proportion of *P. caldenia* pods in cattle diets, was located near the origin of the first axis, whereas cluster B with a high proportion of non-preferred grasses in cattle diets was at the other extreme. All clusters indexing vizcacha diets occupied intermediate positions on the first axis. Diets of cattle, with the exception of those included in cluster C, were found on the lower half of the second axis. The diets of vizcacha were concentrated on the upper half of the second axis. The ordination confirmed our interpretation of the cluster analyses and also revealed higher level of homogeneity in the diets of vizcacha than in cattle.

Diversity indices.

Diversity indices (Fig. 5) exhibited some similar patterns between the 2 herbivores. Cattle indices showed more variability and reached higher values than vizcacha. During the first 7 months of the study, diversity remained low and fairly constant, especially in the case of vizcachas. There was a sharp increase from May to August, more pronounced in cattle than in vizcacha diets. A decrease occurred between August and October, another increase occurred in November, and a final decline in December. Low but significant ($P<0.05$) negative correlations between monthly rainfall and diversity of vizcacha diets ($r = -0.53$) and cattle diets ($r = -0.53$) were found. There was also a negative correlation ($P<0.05$) between monthly mean daily temperature and diversity of vizcacha ($r = -0.65$) and cattle diets ($r = -0.55$). Although rains during the study were lower than average and erratic, there was a general association between months with relatively high rainfall and high temperatures, with low diversity indices.

Discussion

The main components of cattle and vizcacha diets were grasses during most of the study. Cattle preference for grasses has been reported in many regions (Johnson 1979, Migongo-Bake and Hansen 1987, Bóo et al. 1993), and Giulietti and Jackson (1986) have also reported vizcachas preferences for grasses. Although cattle predominantly consumed grasses, *P. Caldenia* pods were an important food source from late summer through the fall. Bóo et al. (1993) reported similar use of *P. Caldenia* pods during a year with well above average rainfall, but they detected a lower level of use (23%) than our study (40%). Menvielle and Hernández (1985) suggest that *P. caldenia* may have special significance as a food resource for cattle during dry years. By consuming pods cattle may expedite seed dispersal and shrub encroachment in the Caldenal (Peláez et al. 1992, Bóo et al. 1993). Pods were not found in vizcacha diets, so these rodents are probably not a dispersal agent of *P. caldenia*.

P. napostaense and *S. tenuis* were present in cattle diets throughout the study, with a very high consumption made of *P. napostaense*. Cattle made a shift to less preferred grasses in November and December 1995. A less pronounced but similar trend was observed for *P. napostaense* in vizcachas. Vizcachas con-

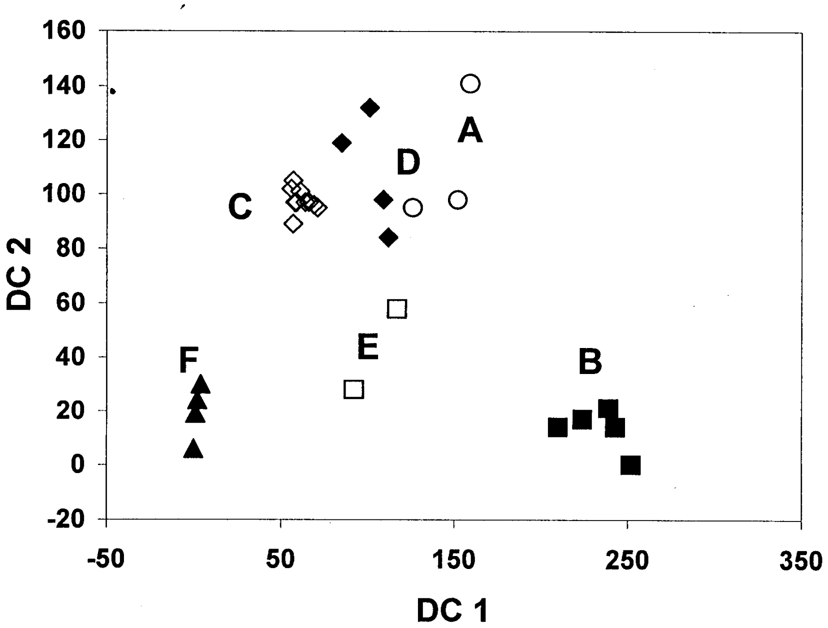

Fig. 4. Spatial distribution of monthly diets defined by the first 2 axes of ordination (DC1 and DC2). Monthly diet of different clusters produced in the classification are: Cluster A: O, Cluster B: g , Cluster C:◊ , Cluster D: u , Cluster E: r and Cluster F: ▲.

sumed more *S. tenuis* in 1995 than in 1994, and they exhibited a less substantial shift to the less palatable *S. speciosa.* This was reflected in the classification and ordination analyses, where vizcacha and cattle diets of November and December 1994 clustered together, but their diets were well separated in these same months in 1995. This was probably due to variations in forage availability, since plant growth was lower in 1995. The drought period that began in April, and continuous heavy grazing, probably caused a decline in available forage and brought about a greater reliance on less preferred forages.

Branch et al. (1994) reported that vizcachas relied heavily on *P. napostaense* throughout the year. We had similar findings for both vizcacha and cattle. The more stable vizcacha diets, compared to cattle, may be related to differences in mouth size and morphology. Cattle may be constrained by bite size and their demands as bulk grazers (Schwartz and Ellis 1981). Size, morphology and grazing behavior may also explain the rapid shift to preferred grasses in vizcachas that was detected in December (Fig. 2) after abundant rains in November 1995 stimulated forage growth.

Cattle grazed less preferred grasses during the dry period of the study, and these species are consumed only when better quality forage becomes scarce (Cano 1975). It is important, in terms of management and planning, to take into account the combined effects of heavy grazing by cattle and vizcachas. Under severe grazing conditions some species (*P. napostaense* and *S. tenuis*) are more tolerant of defoliation than others (*Stipa Clarazii* and *Poa ligularis*). Less tolerant forages may be replaced by undesirables like *S. gynerioides* and *S. tenuissima* (Distel and Bóo 1995).

Forbs were found in low proportions in the diets of both herbivores. Annuals like *M. minima* and *Erodium cicutarium* may provide good seasonal forage during spring (Fresnillo-Fedorenko 1990) in the southern Caldenal. Being annuals, they produce numerous seeds (Mayor 1996), and growth is quite variable between dry and wet years. During a wet year, *M. minima* contributed heavily to cattle diets (Bóo et al. 1993). In our study forb production was low. *M. minima* pods contributed more heavily to vizcacha than cattle diets, possibly because the pods are difficult for cattle to pick up.

Although high diet overlap (90%) occurred between both herbivores in November 1994 through January 1995, exploitative competition cannot be assessed (Begon et al. 1986). During this period rains occurred and stimulated the growth of preferred grasses. During the dry period of the study, cattle and vizcacha diets diverged (Figs. 3 and 4) in qualitative and quantitative terms (Fig. 2). We assume then that the greatest competition for preferred grasses (i.e. *P. Napostaense* and *S. Tenuis*) coincided with the lower levels (38–48%) of dietary overlap. At that time vizcachas, and especially cattle, were forced to rely on the less preferred grasses (i.e. *S. Speciosa, S. Gynerioides,* and *S. Tricotoma*) that have low nutritive value (Cano 1988). This would probably

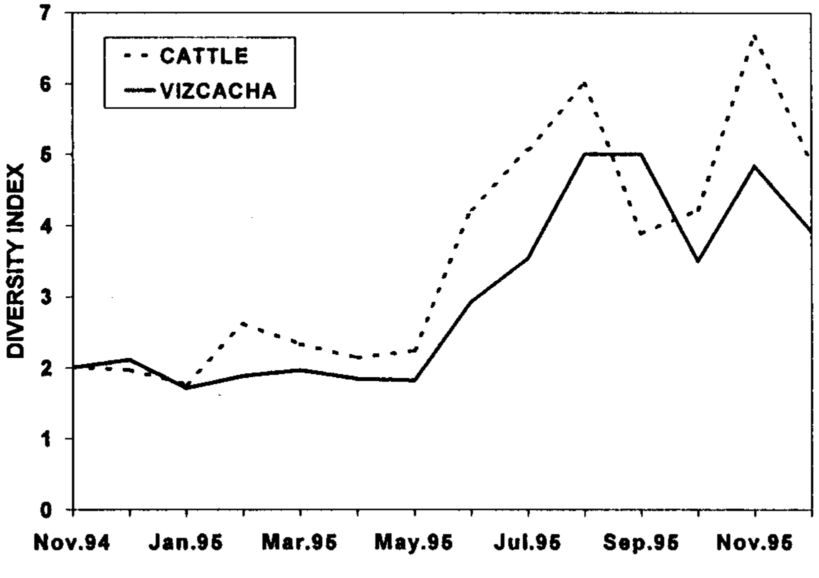

Fig. 5. Monthly diversity indices of cattle and vizcacha's diets sampled in a 600 ha pasture in southeast La Pampa from November 1994 through December 1995.

affect cattle performance more than vizcachas, because the cattle relied more heavily on the lower quality herbage

Holechek et al. (1982) reported an increase in the diversity of cattle diets as forage availability increased in late spring. Because forage biomass depends on rainfall (Sala et al. 1988), one would expect a positive correlation between diversity of the diets and rainfall. Bóo et al. (1993) found no correlation between diversity and rainfall. Kufner and Pellizza de Sbriller (1987) found a higher trophic diversity in cattle and mara (*Dolichotis patagonum*) diets in the arid plains of eastern Mendoza during summer, which was considered the lean season. In our study the warmest months coincided with the highest rainfall. Consequently, there was more forage available than in the coldest and driest months. The negative correlation found among mean monthly daily temperatures, monthly rainfall and botanical diversity of the diets indicated that diversity increased as available forage decreased. When favorable conditions for plant growth occurred, vizcachas and cattle consumed mainly preferred grasses. Under unfavorable conditions their diets diverged because cattle shifted to other resources.

In a study on vizcacha diets Branch et al. (1994) found a decrease in diet breadth concomitant with scarce resources in the field. A decrease in selectivity occurred when annual forbs were abundant. In our study, higher diversity indices occurred during the drier months. This may have been due to a less diverse plant community on our study site than on the natural reserve where Branch's research was conducted.

Cattle and vizcachas have overgrazed our study site for years, and highly preferred grasses like *S. clarazii* and *P. ligularis* are scarce. Monthly diversity was generally lower for vizcacha than for cattle diets, especially during most of the driest months. Vizcachas also consistently consumed more of the preferred grasses and *M. minima* fruits than cattle. We speculate that vizcacha require a higher quality diet than cattle.

Conclusions

This study indicates that both herbivores relied heavily on grasses, with high intake of the available, good quality species during wet and warm months. During the dry months, when the best grasses were scarce, both herbivores grazed on less preferred and lower quality grasses. Managing stocking rate and rodents density should prevent an extreme situation of forage depletion. A low density of vizcachas would also increase availability of desirable grasses for cattle during the wet season.

Prosopis caldenia pods were the only contribution by woody species to cattle diets, and they were not detected in vizcacha feces. While pods could potentially be a good source of food for cattle during the fall, the possibility of seed dispersal and *P. caldenia* encroachment represents a serious risk.

Dietary overlap was highest during wet months when *Piptochaetium napostaense* was consumed in high proportions by both herbivores. Dietary overlap was lower during the fall than during summer because cattle relied on *Prosopis caldenia* pods. The lowest overlap was observed during the driest months when cattle consumed more of the less preferred grasses than vizcacha.

In this study, diversity indices were higher in cattle than in vizcacha diets. During the drier months, diversity of both herbivore diets was higher, because they consumed more of the less preferred species. The combined effect of heavy grazing by cattle and vizcachas should be prevented to avoid displacing high quality forages with undesirable grasses or woody vegetation. These shifts in community composition would be difficult to reverse.

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52:378–383

Consumption of low larkspur (*Delphinium nuttallianum)* by cattle

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Abstract

Low larkspur (*Delphinium nuttallianum* Pritz.) is a toxic range plant that is often fatal to cattle when ingested during spring or early summer on foothill or mountain rangelands. Grazing trials near Price, Ut. during 1996 and 1997 examined toxicity and consumption of low larkspur by cow-calf pairs. Toxic alkaloid concentrations were relatively stable although larkspur plants rapidly matured. Cows and calves did not differ (P>0.1) in consumption of low larkspur (0.6 and 1.1% of bites, respectively), and calves began eating low larkspur readily (up to 21% of bites) early in the trial. Larkspur density did not affect consumption by cattle (P>0.1), but there was an interaction between density and day, as on 2 days (days 8 and 21) cattle ate more (P<0.05) low larkspur in the pastures with more larkspur. Stage of growth also affected consumption (P<0.05) with greater consumption after flowering. Increased grazing pressure caused cattle to eat more larkspur until larkspur density was reduced by grazing. Cattle apparently avoid eating low larkspurs before flowering, and cattle may eat little low larkspur if sufficient other forage is available. Losses may be reduced by ensuring that grazing pressure and/or stock density are not excessive on low larkspur-infested rangelands.

Key Words: cattle grazing, poisonous plants, alkaloids, diet selection

Resumen

"Low larkspur" (*Delphinium nuttallinum* Pritz.) es una planta tóxica que a menudo es mortal para el ganado cuando la consume en primavera o inicio del verano en pastizales de montaña o de pie de montaña. Durante 1995 y 1996 se condujeron ensayos de apacentamiento cerca de Price, Ut. en los que examinamos la toxicidad y consumo de "Low larkspur" por parejas de vaca-becerro. Las concentraciones de alcaloides tóxicos fueron relativamente estables a pesar de que las plantas de "low larkspur" maduraron rápidamente. Las vacas y los becerros no difirieron (P>0.1) en el consumo de "Low larkspur" (0.6 y 1.1% de mordidas respectivamante) y en el ensayo, los becerros comenzaron a comer "low larkspur" más temprano (hasta 21% de mordidas). La densidad de "Larkspur" no afectó el consumo por el ganado (P>0.1) pero hubo una intracción entre densidad y día, en 2 días (días 8 y 21) el ganado consumió mas "low larkspur" (P<0.05) en los potreros con mayor cantidad de "Low larkspur". La etapa de desarrollo del "Low larkspur" también afectó el consumo (P<0.05) siendo mayor después de floración. Incrementos en la presión de apacentamiento causo que el ganado consumiera mas "larkspur" hasta que la densidad de "larkspur" fue reducida por el apacentamiento. El ganado aparentemente evito el consumo de "Low larkspur" antes de la floración y puede consumir poco "low larkspur" si otros forrajes estan disponible en suficiencia. Las pérdidas pueden ser reducidas al asegurar que la presión de apacentamiento y/o la densidad de carga animal no son excesivas en pastizales infestados de "Low larkspur".

Low larkspur (*Delphinium nuttallianum* Pritz.) is a low-growing shallow-rooted perennial plant often implicated in livestock deaths during spring and summer. Low larkspurs generally occur on foothill or mountain ranges, and may initiate growth before other forage species. Availability of low larkspurs may be cyclic, as plant density and seasonal longevity are influenced by precipitation patterns and temperature (Majak and Engelsjord 1988). Inouye and McGuire (1991) reported that timing and abundance of flowering in low larkspurs depends on winter snowpack. Death losses to low larkspur are sporadic, and cattle losses can be severe at times.

The toxins in low larkspur are diterpenoid alkaloids, with most of the toxicity attributed to methyllycaconitine (Majak 1993, Bai et al. 1994, Manners et al. 1995) and nudicauline (Manners et al. 1995). Low larkspur contains other untested alkaloids that may play a role in mammalian toxicity (Gardner and Panter, unpublished data).

There is little information about cattle grazing of low larkspurs. Thus, the objectives of the present study were to determine (1) when cattle consumed low larkspur in relation to plant phenology and toxicity, (2) whether consumption by cattle is related to larkspur density, and (3) whether grazing pressure influences consumption of low larkspurs.

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Materials and Methods

Trial 1, 1996

The trial was conducted about 18 km northeast of Price, Utah on the western edge of the West Tavaputs Plateau at 2621 m elevation. The 5 ha pasture was enclosed with electric fence. Vegetation was dominated by mountain sagebrush (*Artemisia tridentata* var. *vaseyana* Nutt.), with groves of quaking aspen (*Populus tremuloides* Michx.) occurring near the study pasture. Other important vegetation included mountain dandelion (*Taraxacum officinale* Weber ex Wiggers), arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), longleaf phlox (*Phlox longifolia* Nutt.), mountain brome (*Bromus carinatus* Hooker & Arn.), sedge (*Carex raynoldsii* Dewey), and low larkspur.

Five lactating, mature Hereford x Angus cows with calves were used. Calves were about 3 months old; they were still suckling, but also were fully functioning ruminants and grazed avidly at times. Cattle grazed on the pasture from 30 May to 12 June 1996. The trial ended when cattle ate nearly all the low larkspur in the pasture.

Density of low larkspur was determined at the beginning and end of the trial using 100, 0.25 m^2 plots placed every 15 m along 3 pace transects across the pasture. Forage availability was determined by clipping twenty, 0.25 m^2 plots at the beginning and end of the trial, and separating clipped material into grasses, other forbs, and low larkspur. Shrubs were ignored. Low larkspur phenology was determined weekly using pace transects to record phenology for 100 low larkspur plants. Growth stages of low larkspur were categorized as vegetative, early flower (i.e., flowers apparent but most not opened), flower (i.e., most flowers opened), late flower/pod (i.e., mix of flowers and pods on the same plant), and pod (i.e., nearly all flowers developed into pods).

Bite counts were used to determine animal diets, and categorized as low larkspur, grass and other forbs. Cattle were kept in a corral during the night, and released to graze each day about 0700 hours. Each cow was observed in a predetermined order for numerous 5 min periods; these observations continued during all active grazing periods until 1900 hours. Generally we obtained 30 to 40 min of daily observation time for each cow. Calves were also observed for 5-min periods when actively grazing but calves grazed less often than cows.

A composite sample of > 20 individual low larkspur plants was collected weekly for alkaloid analysis. Plants were collected fresh, frozen in plastic bags, freeze-dried, and ground through a 1-mm screen. Larkspur samples were analyzed for toxic alkaloids (methyllycaconitine, 14-deacetylnudicauline, barbinine, and nudicauline/geyerline) using electrospray mass spectrometry methods similar to that described by Marko and Stermitz (1997) with modifications to make the method quantitative. Ground plant material (100 mg) was extracted with 5 ml absolute methanol for 18 hours by mechanical rotation. Reserpine was added as an internal standard and mixed with the sample for an additional 15 min. A 50 µl aliquot of the sample was added to 1.5 ml of methanol/1% acetic acid (1:1) and the sample analyzed by flow injection electrospray mass spectrometry (Gardner, unpublished data).

Trial 2, 1997

We hypothesized that low larkspur is selected as encountered by cattle, and that higher densities would be reflected in higher consumption by cattle. The trial was conducted approximately 30 km southwest of Price, Ut. on Gentry Mountain on the eastern edge of the Wasatch Plateau at 2,650 m elevation. Four, 6-ha pastures were delineated based on density of low larkspur and 2 replicate pastures were designated as either high density (7–9 larkspur plants/m^2) or moderate density (3–5 larkspur plants/m^2). Initial density was determined before grazing began using 250, 0.5 m^2 plots located in each pasture along pace transects. Dominant vegetation in the area was aspen, sagebrush, mountain dandelion, mountain brome, and low larkspur. Aspen stands occurred in every pasture.

On 11 June 1997, 2 cow-calf pairs were randomly placed into each pasture. Cows were 3 to 4 yrs old, and the suckling calves were about 6 weeks old when the 21-day study began. Bite counts were done as described in the previous trial.

Standing crop was determined at the beginning of the trial by clipping, drying and weighing material from 20 plots as described above for Trial 1. Similarly, composite collections of low larkspur plants were made weekly for alkaloid analysis. Larkspur phenology was determined weekly using pace transects as described for Trial 1.

Trial 3, 1997

The cattle from Trial 2 were used at the same location in a 7-day study to determine the effect of grazing pressure on low larkspur consumption. We hypothesized that low larkspur consumption would increase over days as standing crop was reduced. A 3.5 ha pasture was delineated with electric fence, and forage availability was determined by clipping thirty, 0.25 m^2 plots, and drying and weighing the clipped material (i.e., grasses, forbs, and larkspur). All 8 cow-calf pairs were placed into the pasture on 1 July 1997, and bite counts conducted until 7 July 1997, as previously described. Low larkspur phenology and density were determined at the end of the trial using pace transects as previously described. A composite sample of > 20 low larkspur plants was also collected at the beginning and end of the trial to determine alkaloid concentration.

Statistical analysis

Consumption of low larkspur by cows and calves in Trial 1 was compared over days using the GLM procedure of SAS (1988). The repeated measures model included type of animal (i.e., cows vs. calves), individual animals nested within type (error a), with repeated measures over the 14 days of the trial. During Trial 2, calves ate no larkspur so they were not compared to cows. The repeated measures model for Trial 2 included larkspur density (high vs. moderate), pasture (i.e., replication), density x pasture, stage of growth (i.e., flower vs. pod), day nested within stage, pasture x stage, pasture x day within stage, density x stage, density x day within stage, density x pasture x stage, and density x pasture x day within stage. The pasture and density x pasture terms were added to test density effects, the pasture x stage and pasture x day within stage were added to test for stage effects, and the last 2 interaction terms were summed to test the density x stage and density x day within stage interactions. Significant interactions ($P< 0.05$) were examined using the PDIFF procedure of SAS (1988). Trial 3 was analyzed using an ANOVA model that included animals as blocks and days as the treatment effect.

Results

Toxic alkaloid concentrations

Toxic alkaloid concentrations were relatively stable (Table 1), particularly for methyllycaconitine, although larkspur plants rapidly matured during the studies (Table 2). Concentrations of nudicauline decreased as low larkspur plants matured during 1996, and after an initial reduction early in 1997, concentrations remained relatively stable after flowering even in senesced plants. Very low concentrations of 14-deacetylnudicauline and barbinine (a minor toxic alkaloid) were found in all plant samples. The dry matter content of individual low larkspur plants ranged from 21% in the early flower stage to 55% in the late pod stage; individual plants ranged in dry weight from 0.2 to 0.65 g/plant.

Table 1. Concentration (mg/g, dry weight) of toxic alkaloids in low larkspur (*Delphinium nuttallianum*) during 3 grazing trials in central Utah.

Date	Phenological Stage[2]	Toxic Alkaloid[1] MLA	DAN	NUD	Barbinine
		(mg/g)			
Trial 1-1996					
21 May	Early Flower	1.9	<0.5	1.6	<0.5
30 May	Early Flower	1.2	<0.5	1.0	<0.5
6 June	Flower	1.4	<0.5	1.0	<0.5
12 June	Late Flower/Pod	1.8	<0.5	1.1	<0.5
Trial 2-1997					
20 May	Vegetative	1.6	<0.5	1.5	<0.5
12 June	Early Flower	1.0	<0.5	0.8	<0.5
19 June	Early Flower/Flower	1.1	<0.5	0.7	<0.5
26 June	Flower/Early Pod	1.3	<0.5	0.9	<0.5
Trial 3–1997					
3 July	Flower/Early Pod	1.2	<0.5	0.8	<0.5
3 July	Pod	1.3	<0.5	0.6	<0.5
7 July	Flower/Early Pod	1.6	<0.5	0.6	<0.5
7 July	Pod	1.3	<0.5	0.4	<0.5
7 July	Shattered	1.1	<0.5	0.6	<0.5

[1]N-methyl succinimido anthranoyllycoctonine (MSAL) type alkaloids that are the dominant toxic alkaloids in low larkspurs. MLA=methyllycaconitine; DAN=14-deacetylnudicauline; NUD=nudicauline and a closely related isomer, geyerline. 14-deacetylnudicauline and barbinine occurred in all samples but concentrations were very low.
[2]Early flower/flower=flowers apparent but not open; flower/early pod=mix of flower and pod on the upper and lower portion of the stem, respectively.

Trial 1, 1996

Low larkspur density was 2.5 plants/m^2 when the trial began, and forbs dominated the available forage (Table 3). Low larkspur comprised roughly 1% of the available forage; similarly cows selected 0.5 to 2% of their bites as low larkspur during the first week of the trial. The cattle consumed most of the low larkspur plants in the pasture and larkspur density was 0.3 plants/m^2 when the trial ended. Cows and calves did not differ (P>0.1) in consumption of low larkspur (0.6 and 1.1% of bites, respectively), even though some calves began eating low larkspur readily in the early days of the study (Fig. 1). Individual calves ate a maximum of 16 to 21% of their bites as low larkspur in the first 2 days of the study; during some grazing bouts larkspur consumption exceeded 50% of their bites. Overall, cows and calves selected remarkably similar (P>0.1) amounts of grass (84 and 83% for cows and calves, respectively) and forbs (15 and 14%, for cows and calves, respectively).

Trial 2, 1997

The experimental pastures were similar in available forage except for amounts of low larkspur. There was a stage of growth effect (P<0.001) for low larkspur consumption as cattle ate more larkspur after larkspur flowered. Few larkspur plants had flowered during the first week of the trial, and cattle took only a few bites of low larkspur before most plants had fully flowered (Fig. 2). Cattle ate <1% of their bites as low larkspur during the preflower and flower stages, but as low larkspur matured into the late flower/pod stage consumption increased to 2.5% of bites. There was a density x day within stage interaction (P<0.01), but the main effect of density was not significant (P>0.1). The density x day within stage interaction occurred because on day 8 during the preflower/flower period cattle in the high density pasture averaged over 5% low larkspur bites, whereas in the moderate density pasture on this day cattle ate almost no low larkspur. Furthermore, during the late flower/pod stage on day 21, cattle in the high density larkspur ate almost 10% of their bites as low larkspur, whereas cattle in the moderate density pasture ate <1% of their bites as low larkspur. Although cattle in the moderate density pasture appeared to eat more larkspur on days 15 to 19, these differences were not significant (P>0.1), and consumption of low larkspur by cattle in the moderate density treatment was near zero when the trial ended on day 21.

Table 2. Phenology of low larkspur during summer, 1996 and 1997 in central Utah. Each value is the percentage of plants in the respective growth stage on the sampling date.

Trial/Date	Growth Stage: Vegetative	Early Flower[1]	Flower	Late Flower/ Early Pod[2]	Pod
	(%)				
Trial 1, 1996					
5/30	0	77	20	3	0
6/6	0	7	71	13	9
6/12	0	0	0	65	35
Trials 2 & 3, 1997					
6/11	38	59	3	0	0
6/20	0	21	79	0	0
6/26	0	0	48	52	0
7/7	0	0	0	5	95

[1]Flowers apparent but not open
[2]Mix of flower and pod on the upper and lower portion of the stem, respectively

Trial 3, 1997

Cattle diets differed over time as the forage standing crop was reduced. Consumption of low larkspur peaked on day 4 ($P<0.05$) and was lowest on day 7 (Fig. 3) as larkspur was depleted from the pasture. Forb consumption was highest ($P<0.05$) during the first 2 days (7 to 9%) and then fell to <2% during the rest of the trial. Low larkspur and forb consumption both averaged about 3% during the 7-day trial, whereas grass consumption averaged 93% (range 88 to 96%, $P<0.05$).

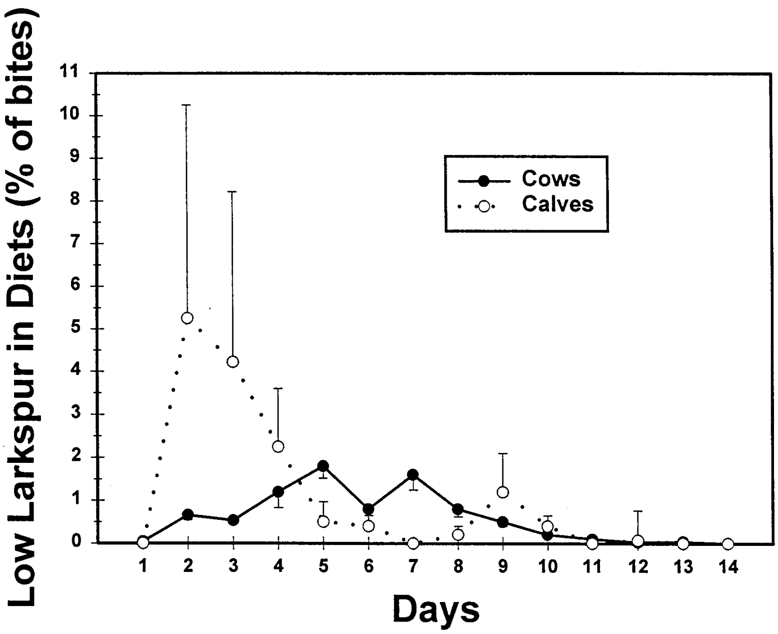

Fig. 1. Consumption of low larkspur (% of bites ± SE) by cows and nursing calves during an early summer (30 May to 12 June) grazing trial near Price, Ut., 1996.

Discussion

Our visual observations during the 1996 trial suggested that cows did not prefer or avoid low larkspur, but rather consumed larkspur in relation to availability in the pasture. Consumption decreased to nearly zero as larkspur density declined from grazing, suggesting that cattle were not actively searching for low larkspur plants.

Calves grazed much more sporadically than cows in 1996, but during the initial days of the study the naive calves appeared to prefer low larkspur. Nonetheless, calves generally ate little low larkspur after day 4 for reasons that are not clear. It is possible that calves ingested sufficient low larkspur early in the study to induce mild intoxication, forming a temporary aversion to larkspur (Pfister et al. 1997a); however, we saw no clinical signs of poisoning in grazing calves. Alternatively, calves may have also been responding to decreasing low larkspur density and/or growth of other forage plants. Calves ate no larkspur during the 1997 summer trial, probably because they were younger by 6 weeks and appeared to graze much less than did the calves used in 1996.

Larkspur density during the 1997 density trial influenced consumption by cattle on only 2 of 21 days. Because the density trial began when low larkspur was vegetative or in the early flower stage, and other forages were still initiating growth, the experimental pastures were purposely made sizable so that selection was not impeded. In general, low larkspur consumption was low during the trial, and larkspur density was not an important factor on most days. Nonetheless, on days when cattle did eat significant amounts of low larkspur, most of that consumption occurred in the high density rather than low density pastures. This suggests that density may be important during those times when low larkspur is palatable and eaten in relatively large amounts by grazing cattle. It is not clear what other environmental or forage factors were positively or negatively influencing cattle consumption of low larkspur during the density trial.

The grazing pressure trial suggested that amount of available forage and the relative amount of low larkspur are major factors influencing consumption of low larkspur by cattle. These results must be interpreted cautiously, however, because of the short duration of the trial. Concentrating cattle in the smaller pasture immediately increased the amount of low larkspur eaten, as cows that had previously taken few bites of larkspur began to consume larkspur in greater amounts. It is possible that social facilitation was also a factor in increased consumption; consumption increased within a few hours after the trial began for some cows that previously had eaten little larkspur. Consumption of low larkspur reached a peak on day 4 when other forage was declining in abundance, and then low larkspur consumption decreased as the amount of low larkspur in the pasture also declined.

Low larkspurs matured rapidly during both summers, and generally developed from the early flower stage (flowers visible but not open) to the late flower/pod

Table 3. Standing crop (kg/ha ± SE) during low larkspur grazing trials during summer, 1996 and 1997 in central Utah.

Forage Class	Sample Period	
Trial 1, 1996	Begin[1]	End[1]
	-(kg/ha)-	
Grass	70 ± 10	111 ± 13
Forbs	246 ± 37	110 ± 15
Larkspur	30 ± 4	3 ± 2
Trial 2, 1997	Begin: High Pasture[2]	Begin: Moderate Pasture[2]
Grass	197 ± 16	172 ± 18
Forbs	34 ± 8	35 ± 9
Larkspur	67 ± 12	18 ± 6
Trial 3, 1997	Begin[3]	End[3]
Grass	198 ± 29	76 ± 7
Forbs	48 ± 18	8 ± 5
Larkspur	38 ± 12	6 ± 2

[1]Trial 1 began on 30 May, 1996 and ended on 12 June, 1996
[2]Trial 2 began on 11 June, 1997 with standing crop averaged over 2 replicate pastures for both the High Density and Moderate Density treatments; no end clip was done as forage was abundant on all pastures.
[3]Trial 3 began on 1 July, 1997 and ended on 7 July, 1997; the pasture included portions of both high and moderate density pastures used during Trial 2.

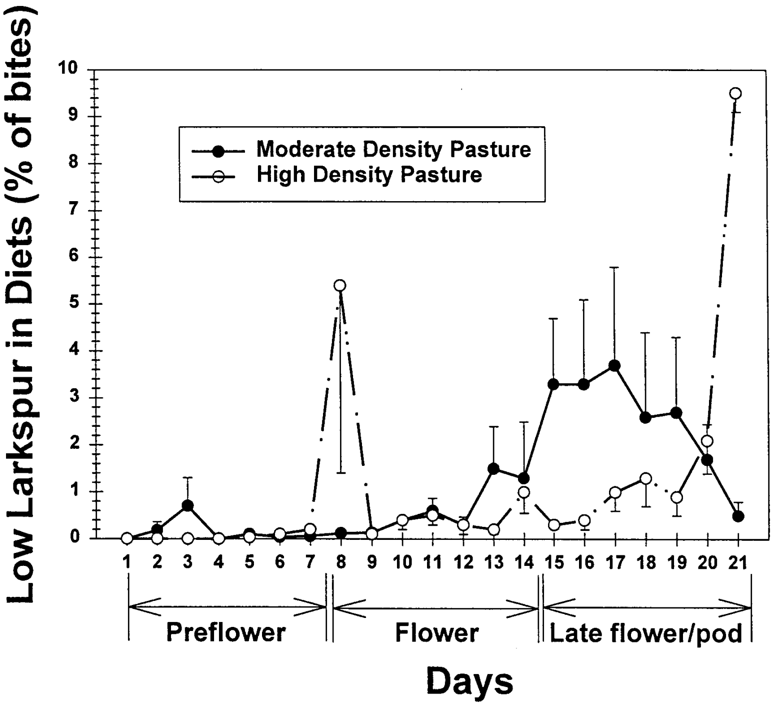

Fig. 2. Consumption of low larkspur (% of bites ± SE) by cows grazing in pastures containing either moderate or high densities of low larkspur during summer (11 to 30 June) near Price, Ut., 1997. Dominate low larkspur phenology is indicated below the x-axis.

stage (mix of mature flowers and immature pods on each stem) within 14 to 21 days. Inouye et al. (1991) reported that there was an 18 day interval between first and last flowering in *D. nelsonii* growing at 2,900 m elevation in Colorado. Majak (1993) found that methyllycaconitine concentration declined substantially as low larkspur matured from the vegetative to reproductive stages of growth, but was relatively stable thereafter. Further, Majak et al. (1987) reported that nudicauline was a relatively minor alkaloid in low larkspur with a concentration < 0.5 mg/g, although roots and seed pods were substantially higher in nudicauline compared to leaves and stems (Majak and Engelsjord 1988). In our studies, the toxic alkaloid concentration of low larkspurs was relatively low but stable in maturing plants; even dry, shattered low larkspur plants retained over 1 mg/g of methyllycaconitine in addition to low concentrations of nudicauline. This relative stability contrasts with tall larkspur alkaloid concentrations which usually decrease greatly with maturity (Pfister et al. 1994, Ralphs et al. 1997).

When ingested by cattle, each low larkspur plant formed a single bite, regardless of plant height. Low larkspur plants taller than 15 to 20 cm were simply folded into the cow's mouth, and both short and tall plants were usually broken off near ground level whatever the height or stage of growth. These observations contrast with those of Majak and Engelsjord (1988), who suggested that cattle ate only the upper portion of the low larkspur plants.

Cattle typically show clinical signs (i.e., tremors and periodic collapse) when given a methyllycaconitine + 14-deacetylnudicauline dose from tall larkspur (*D. barbeyi*) of about 20 mg/kg b.w. Nudicauline has not been found in tall larkspur, and is about twice as toxic per unit of weight compared to methyllycaconitine or 14-deacetylnudicauline (Manners et al. 1995). Assuming an average dry weight per plant of 0.5 g, and also assuming a methyllycaconitine + 14-deacetylnudicauline concentration of 1.5 mg/g, plus a nudicauline concentration of 1 mg/g (dry wgt), low larkspur plants would contain a toxic alkaloid concentration equivalent to 3.5 mg/g plant dry weight [methyllycaconitine + 14-deacetylnudicauline + (nudicauline x 2)]. Thus, a 450 kg cow may show clinical signs after eating 2.5 kg (dry weight) of low larkspur. Cattle would need to eat about 20% of their daily diet as low larkspur to become intoxicated, given a dry matter intake of 13 kg/day.

Viewed in a different way, cattle in our grazing studies on mountain ranges often have a biting rate of 50 bites/min or 24,000 total bites during active, daylight grazing hours. A cow in this scenario would have to eat about 5,000 bites of low larkspur in a single day to

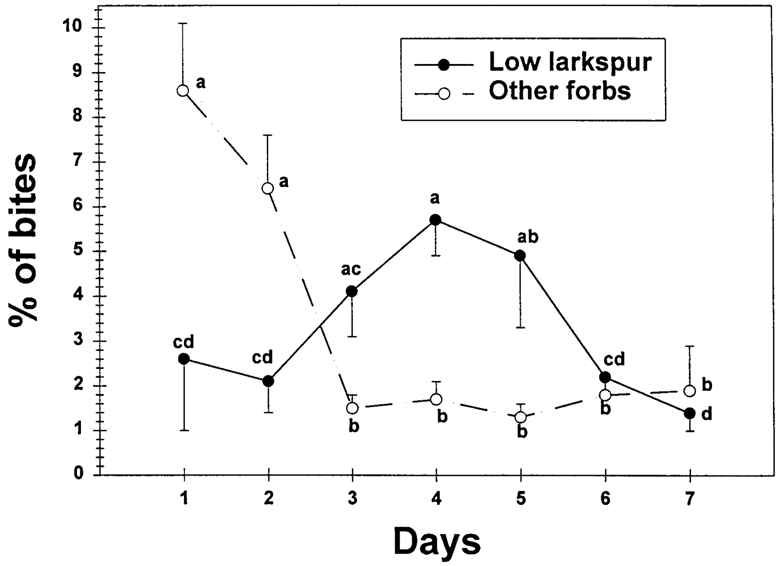

Fig. 3. Consumption of low larkspur (% of bites ± SE) by cows grazing in a single pasture during a grazing pressure trial to deplete available forage during summer (1 to 7 July), near Price, Ut., 1997. Different superscript letters within each plant category indicate significant differences between days (P<0.05).

be poisoned. We estimate that the greatest number of total larkspur bites by any individual cow that we observed in 1997 was about 3,000 bites (≈1.5 kg) in a single day. We did not observe any indications of clinical toxicity in cows in our grazing studies, and our bite counts showed that their diets did not approach a toxic dose.

Our results suggest that cattle eat only small amounts of low larkspur before flowering, as we have noted with tall larkspurs (Pfister et al. 1997b), and that cattle may eat little low larkspur if sufficient other forage is available. Further, we suggest that losses may be reduced by ensuring that grazing pressure and/or stock density are low. Additional research will be necessary to confirm these findings. Because low larkspurs are short-lived plants (4 to 6 weeks), for many livestock producers the management scheme of choice may be to simply wait until low larkspurs are very mature, and other forage is abundant, before placing cattle in heavily infested pastures. On moderate- to high-elevation (> 2,500 m) ranges, onset of flowering in low larkspurs may coincide with the growth of adequate amounts of other forage to support moderate stocking rates. More information on factors influencing cattle to eat low larkspurs is clearly needed, and research will continue on such aspects as the relationship between consumption, larkspur and forage phenology, particularly early in the season, and forage availability.

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Technical Note:
Pericarp removal has little effect on sagebrush seeds

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Abstract

Sagebrush (*Artemisia*) is commonly recommended for reclamation and restoration of shrublands of the Western United States and seeds are usually obtained from commercial sources. One result of commercial seed processing is the removal of the pericarp. We tested 2 seedlots of Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) to determine if pericarp removal affected properties of seed hydration or seed germinability under different levels of water stress. In general, pericarp removal had a relatively minor effect on these processes and properties.

Key Words: *Artemisia tridentata* ssp. *wyomingensis,* germination percentage, germination rate, humidification, water stress

Resumen

"Sagebrush" (*Artemisa*) es comúnmente recomendada para la recuperación y restauración de áreas invadidas con arbustos en el oeste de los Estados Unidos y la semilla utilizada usualmente se obtiene de fuentes comerciales. Uno de los resultados del procesamiento comercial de semilla es la remoción del pericarpio. Probamos dos lotes de semillas de "Wyoming big sagebrush" (*A. tridentata* Nutt. spp. *wyomingensis* Beetle & Young) para determinar si la remoción del pericarpio afecta la propiedades de la hidratación y germinabilidad de la semilla bajo diferentes niveles de estrés de agua. En general, la remoción del pericarpio tuvo un efecto relativamente menor en estos procesos y propiedades de la semilla.

Pericarp removal is a side effect of commercial seed processing of sagebrush (*Artemisia*) (Welch 1995, Booth et al. 1997). Reclamationists are concerned that over-processing of sagebrush seeds by industrial debearders may contribute to poor seedling establishment. While seed germinability under optimal germination conditions is not affected by standard commercial procedures (Booth et al. 1997), it is unknown how pericarp removal influences seed germination under water stress.

Seed hydration treatments have been used to improve germination rate of many agricultural and rangeland species (Bleak and Keller 1974, Heydecker and Coolbear 1977, Hardegree 1996). Bai et al. (1997) found that presowing humidification did not improve seed germinability of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) but these tests were conducted under optimal moisture conditions. The objectives of this study were to examine the effects of pericarp removal on water uptake during humidification and on subsequent germination of Wyoming big sagebrush seeds under water stress.

The research was funded by the Wyoming Abandoned Coal Mine Reclamation Program. Dr. Gary Richardson was our statistical consultant. Mention of trade or company names is for information only and does not imply an endorsement.
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Materials and Methods

Two seedlots, harvested in late October 1993, were obtained from a commercial supplier. Seedlot 1 was collected in Lincoln County, Wyo. at 2,044 m elevation. Seedlot 2 was collected near Casper, Wyo. at 1,624 m elevation. Seedheads were stored in large woven polypropylene bags in an unheated warehouse for approximately 4.5 months before being processed with a 48-inch Simon-Day debearder for 10 minutes (Booth et al. 1997). Seeds were stored at room temperature in a laboratory after processing and were 21-months old at the time of the study.

Seeds (achenes) with pericarp were separated from those without pericarp by hand sorting. Sets of 20 seeds from each seedlot were placed in 0.25 ml tin capsules for determination of initial weight (Booth and Bai 1998). The capsules were held upright in an open rack inside of a sealed 32 x 19 x 18 cm plastic box. Water was added to the box to a depth of 10 cm, 1-cm below the level of the capsules, and the box placed in an incubator at 10°C. Seed capsules were retrieved from the plastic box after 0, 8, and 48 hours of humidification, sealed and weighed. The seed capsules were then opened, dried in an oven for 24 hours at 80°C and reweighed to determine seed moisture content. Each humidification treatment was repeated 9 times for each seedlot in a completely randomized design.

Humidified seeds were germinated under different levels of water stress using the matric-potential control system described by Hardegree and Emmerich (1992). In this system, seeds are equilibrated on top of a cellulose membrane that is in contact with an osmotic solution of polyethylene glycol 8000 (PEG) inside a clear plastic snap-top vial. Matric potential on top of the membrane is controlled by adjusting the concentration of the PEG in the solution reservoir under the membrane. PEG was mixed with water to obtain solutions with a water potential of 0, –0.25, –5, –0.75, –1.0, –1.25 and –1.5 MPa (Hardegree and Emmerich 1990).

Nine sets of 20 seeds each were evaluated for each combination of treatment and water stress level. Seeds were first held at 5°C in darkness for 4 days and then incubated at 20°C with a 12 hour photoperiod under fluorescent and incandescent lights for an additional 14 days. No seeds germinated during the 4-day imbibition period at 5°C. Germination was checked daily and seeds were counted and removed when they exhibited radicle extension of ≥ 5 mm. A completely randomized design with 9 replications was used and replications were arranged in separate incubators.

Two germination indices were calculated: total germination percentage (G); and the actual days required to achieve 50% (D50) of G as an index of germination rate. Seed-moisture-content data were analyzed with ANOVA and LSD mean separation (Snedecor and Cochran 1980). Cubic regression equations were calculated relating G and D50 to water potential for each humidification treatment. Regression equations were recalculated by deleting first cubic then quadratic terms that were not significant ($P>0.10$). Lower order terms that were not significant were left in the equation if a higher level term was significant. Total germination (G) and D50 were estimated from the regression equations and model confidence intervals (95%) were determined for each treatment combination (Evans et al. 1982). Treatment effect was considered significant if the confidence intervals of the equations did not overlap each other. Total germination percentages at –1.25 and –1.50 MPa were excluded from the regression equation because they were less than 1% on average. Days to 50% germination could not be calculated for treatments that did not exhibit some germination. The D50 values were not included in the regression equation if half or more of the replicate samples exhibited no germination, for example, at –1.25 and –1.50 MPa.

Table 1. Seed moisture content of Wyoming big sagebrush after humidification. Values are means ± SE from 9 replications.

Seedlot/type	Humidification duration (hour)		
	0	8	48
	-(%)-		
Seedlot 1			
Non-pericarp	4.95 ± 0.17	21.14 ± 0.45	50.49 ± 1.19
Pericarp	4.95 ± 0.20	20.37 ± 0.31	50.35 ± 1.14
Seedlot 2			
Non-pericarp	5.04 ± 0.13	19.98 ± 0.44	47.77 ± 0.47
Pericarp	4.85 ± 0.08	18.82 ± 0.27	45.98 ± 0.48

Results and Discussion

Seed moisture of both seedlots increased with increased duration of humidification (Table 1). The moisture content of seeds with and without pericarp was not significantly different for seedlot 1 within any humidification duration. Seeds without pericarp absorbed more moisture on a percentage basis after both 8 and 48 hours but only by a few percent. It is likely that the mostly dead pericarp tissue inherently holds less water than living cells inside the hydrating seeds. In any case, these differences are relatively small and do not appear to be biologically significant.

Humidification did not affect total germination (G) or time to 50% germination (D50) of any seedlot or treatment. Data were, therefore, pooled among the 3 humidification treatments for each seedlot. Humidification is similar to other prehydration treatments that have had some success at stimulating germination response (Bleak and Keller 1974). Other studies, however, have generally found better success by equilibrating seeds at lower water potentials and for greater treatment durations (Heydecker and Coolbear 1977, Hardegree 1996). Prehydration seed treatments have also been shown to stimulate germination response under sub-optimal temperature conditions but this was not tested here.

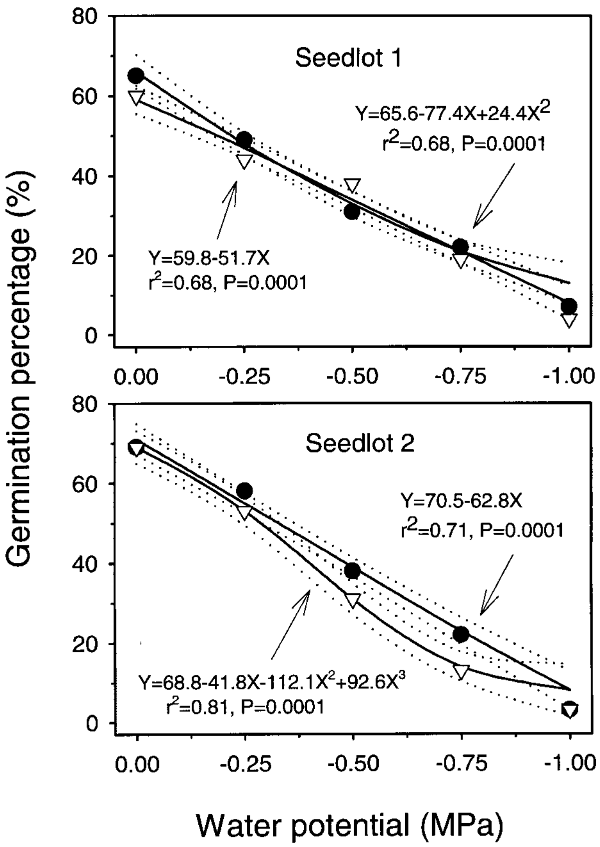

Fig. 1. Predicted germination percentage (solid line) with 95% confidence bands (dotted line) of Wyoming big sagebrush seeds with (filled circles) or without (open triangles) pericarp as a function of water potential. Symbols indicate actual values.

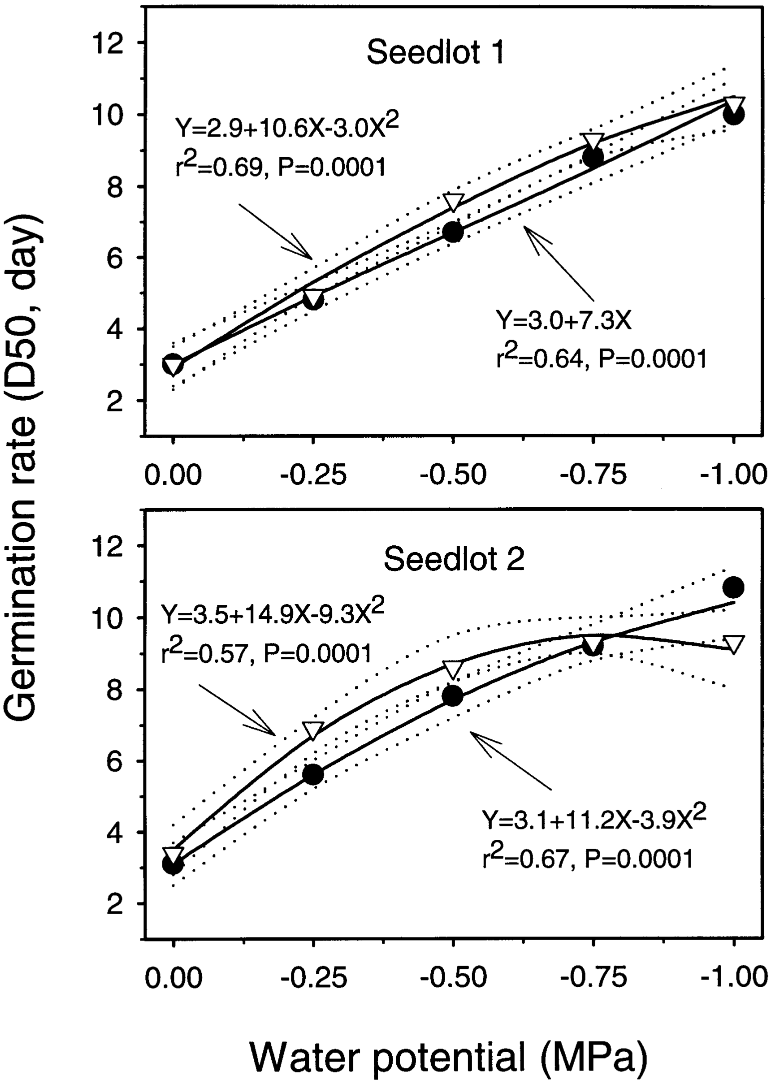

Fig. 2. Predicted germination rate (D50, solid line) with 95% confidence bands (dotted line) of Wyoming big sagebrush seeds with (filled circles) or without (open triangles) pericarp as a function of water potential. Symbols indicate actual values.

Seed germination and germination rate of Wyoming big sagebrush were limited by water stress, similar to basin big sagebrush (*A. tridentata* Nutt.) (Sabo et al. 1979) and fringed sagebrush (*A. frigida* Willd.) (Sabo et al. 1979, Bai et al. 1995). Pericarp removal did not affect germination percentage at any level of water stress for seedlot 1 (Fig. 1). Seeds without pericarp had higher germination percentages at –0.5 and –0.75 MPa for seedlot 2 but separation of confidence interval boundaries was not large. The biological significance of this is probably limited except to say that pericarp removal did not have a negative effect on total germination percentage (G). Welch (1995) tested the viability of sagebrush seeds with or without pericarp using tetrazolium, and found no difference between the 2 groups after as much as 88 months of storage.

Germination rate was also similar between seeds with and without pericarp (Fig. 2). There were some water potentials where germination rate was significantly different but these differences were relatively small.

In summary, pericarp removal did not greatly affect either total germination percentage or germination rate of the 2 seedlots tested. These results confirm that debearder seed processing does not reduce seed quality of Wyoming big sagebrush and is, therefore, unlikely to affect relative success of seedling establishment.

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Responses of winterfat seeds and seedlings to desiccation

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Abstract

Winterfat [*Krascheninnikovia lanata* (Gueldenstaedt) syn. *Ceratoides lanata* (Pursh) J.T. Howell, syn. *Eurotia lanata* (Pursh) Moq.] is a native shrub of mixed prairie of North America. A large portion of hydrated seeds and seedlings can be killed when exposed to seedbed desiccation. Winterfat seeds and young seedlings subjected to varying levels of desiccation were studied to measure the influence of this stress. Germination was unaffected (P>0.05) when seeds were exposed for 0 to 10 hydration-desiccation cycles (2 hours hydration and 22 hours desiccation cycle^{-1} at 20 to 30% relative humidity and 20°C). Linear increases in germination rate (0.6% day^{-1} hydration-desiccation cycle^{-1}), seedling length (0.1 mm hydration-desiccation cycle^{-1}), and seed decay (1.5% hydration-desiccation cycle^{-1}) occurred with an increasing number of hydration-desiccation cycles. Seedling survival following desiccation decreased 10.4% mm^{-1} as seedling length increased from <2mm to 10–15 mm. Seedling survival was positively correlated with relative humidity and negatively correlated with duration of desiccation. The difference ($P \leq 0.05$) in survival between 0 and 90% relative humidity was 62% for seedlings 4–6-mm in length and 70% for seedlings 9–11-mm in length. Seedlings from seeds that germinated rapidly were more tolerant of desiccation than those from seeds germinating slowly. After desiccation in 30% relative humidity, survival of seedlings from seeds germinating on the first day of incubation was 40% greater than those from seeds germinating on the third day of incubation. Electrolyte leakage indicated that desiccation damaged cells. Establishment of winterfat seedlings will be favored by seedbed conditions that protect seedlings from severe and prolonged desiccation and allow fast entry of the radicle into soil.

Key Words: *Krascheninnikovia lanata* (Gueldenstaedt), *Ceratoides lanata* (Pursh) J.T. Howell, *Eurotia lanata* (Pursh) Moq., restoration, seed germination, seed hydration, seedbed ecology.

Resumen

"Winterfat" [*Krascheninnikovia lanatai* (Gueldenstaedt) syn. *Ceratoides lanata* (Pursh) J.T. Howell syn. *Eurotia lanata* (Pursh) Moq.] es un arbusto nativo de las praderas mixtas de Norte América. Un gran proporción de semillas y plántulas hidratadas pueden morir cuando se exponen a la desecación de la cama de siembra. Se estudiaron semillas y plántulas de "Winterfat" sometidas a diferentes niveles de desecación para medir la influencia de este estrés. La germinación no fue afectada (P>0.05) cuando las semillas se expusieron de 0 a 10 ciclos de hidratación-desecación (2 horas de hidratación y 22 horas desecacion ciclo^{-1} y de 20 a 30% de humedad relativa y 20°C). Incrementos lineales en la tasa de germinación (0.6% día-1 ciclo hidratación-desecación^{-1}), longitud de la plántula (0.1 mm ciclo hidratación-desecación^{-1}) y decadencia de la semilla (1.5 ciclo hidratación-desecación^{-1}) ocurrieron con un número creciente de ciclos de hidratación-desecación. La sobrevivencia de plántulas después de la desecación decreció 10.4% mm^{-1} conforme la longitud de la plántula incrementó de <2 mm a 10–15 mm. La sobreviviencia de las plántulas fue positivamente correlacionada con la humedad relativa y negativamente correlacionada con la duración de la desecación. La diferencia en sobrevivencia ($P \leq 0.05$) entre 0 y 90% de humedad relativa fue 62% para plántulas de 4–6-mm de longitud y 70% para plántulas de 9–11-mm de longitud. Las plántulas provenientes de semillas que germinaron rápidamente fueron más tolarantes a la desecación que aquellas provenientes de semillas que germinaron lentamente. Después de una desecación del 30% de la humedad relativa la sobrevivencia de plántulas de semillas que germinaron el primer día de incubación fue 40% mayor que aquellas de semillas que germinaron el tercer día de incubación. La fuga de electrolitos indicó que la desecación daño las células. El establecimiento de plántulas de "Winterfat" sería favorecido por condiciones de la cama de siembra que portejan las plántulas de una desecación severa y prolongada y que permitan la entrada rápida de la radícula en el suelo.

Winterfat [*Ceratoides lanata* (Pursh) J.T. Howell, syn. *Eurotia lanata* (Pursh) Moq., syn. *Krascheninnikovia lanata* (Gueldenstaedt)] is a long-lived, native shrub of northern mixed prairie in North America (Coupland 1950, Romo et al. 1995). Winterfat provides excellent forage (Clarke and Tisdale 1945, Smoliak and Bezeau 1967) and contributes to the structural diversity of rangeland ecosystems (Romo et al. 1995). High seedling mortality has been identified as a major obstacle to seedling establishment (Booth 1992), and desiccation may be an important factor causing seedling death.

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On northern mixed prairie, winterfat diaspores are shed mid-September through October (Romo et al. 1995). Diaspores must after-ripen, and thus do not germinate until the following spring. Many diaspores lodge in plant litter above the soil surface while others lie on the soil surface (Booth 1987, Booth and Haferkamp 1995). Diaspores germinating in early spring during moist conditions (Woodmansee and Potter 1971) may be exposed to alternating periods of desiccation and rehydration. Environmental factors such as litter, microtopography, and neighboring plants can influence moisture conditions immediately surrounding a diaspore or seedling (Fowler 1986, Cheplick and Quinn 1987). Diaspores and seedlings on different microsites may, therefore, experience a wide range of desiccation stress. Response of germinating seeds or seedlings to desiccation varies with developmental stages (Hassanyar and Wilson 1979, McKersie and Tomes 1980, Friedman et al. 1981, Senaratna and McKersie 1983, Hong and Ellis 1992, Allen et al. 1993, Debaene-Gill et al. 1994), implying that biological timing of desiccation is an important aspect of this stress.

Other factors besides desiccation may be responsible for winterfat seedling mortality, including freezing (Hou and Romo 1997, Bai et al. 1998a) and fungal infection. It is, however, difficult to separate these causes in the field. The purpose of this study was to evaluate impacts of desiccation on germinating seeds and young seedlings of winterfat. These experiments characterized effects of: 1) repeated seed hydration-desiccation cycles on winterfat germination and seedling growth; 2) desiccation on survival of different size seedlings, and; 3) desiccation duration and relative humidity during desiccation on subsequent growth and survival of seedlings.

Materials and Methods

Seed collection

Winterfat diaspores were collected in late September 1995 at the University of Saskatchewan, Matador Research Station (50°42'N, 107°43'W, elevation 685 m). This northern mixed prairie has been described by Romo et al. (1995). Diaspores were air dried to about 3–5% water content at room temperature for about 30 days and then stored in plastic bags at –15°C until used.

Experiment I—Effects of hydration-desiccation cycles on seed germination and seedling growth

The hypothesis that repeated hydration and desiccation of diaspores of winterfat reduces germination was tested by exposing diaspores to 0 to 10 hydration-desiccation cycles. Several hundred diaspores were placed on moistened germination paper over plastic slant-boards, and covered with 1 layer of cellulose tissue (Jones and Cobb 1963). Slant-boards were then placed in closed germination boxes (25 x 40 x 20 cm), which were filled with distilled water to a 3-cm depth. These boxes were placed in incubators at 20°C in darkness for 2 hours. One-half of the diaspores were then removed and placed in dry germination boxes with 20 to 30% relative humidity for 22 hours at 20°C, completing 1 hydration-desiccation cycle. These hydration-desiccation cycles were repeated 9 times more giving a range of 0 to 10 cycles. After each hydration-desiccation cycle, water content (dry-weight basis) of 10 hydrated and 10 desiccated diaspores was measured using tin capsules as described by Booth and Bai (1998). Following each cycle, 20 desiccated diaspores were incubated on slant-boards at 20°C in 12 hours light and 12 hours darkness for 7 days, prepared as above. Germination was checked daily between 1 and 7 days, and diaspores were considered germinated if the radicle of seedlings was $\geq$2 mm. The number of diaspores not germinating, but decaying, was determined for each hydration-desiccation cycle. Germination rate was calculated as the sum of total germinated diaspores day^{-1} divided by total germination and multiplied by 100 (Maguire 1962). At the end of the 7-day-incubation period, seedling axial length was determined using a digitizing tablet (Booth and Griffith 1994).

Experimental design was a randomized-complete-block with the 11 hydration-desiccation cycles applied to 4 blocks separated by 1-day intervals. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Regression analyses were performed and best-fit models ($P \leq 0.05$) were selected (Snedecor and Cochran 1980). Untransformed data are presented.

Experiment II—Effects of desiccation on survival of different size seedlings

This experiment was conducted to test the effects of desiccation on seedlings of different sizes. Seeds, removed by hand from diaspores, were soaked in a 600 mM ethanol solution at room temperature for 4 hours, then thoroughly washed in distilled water. This ethanol treatment ensured fast and synchronous germination (Hou and Romo 1998). After ethanol treatment about 300 seeds were placed in 32 x 21 x 7 cm plastic boxes lined with 6 layers of germination paper wetted with 120 ml distilled water, and incubated at 18°C in darkness. On the fourth day of incubation seedlings were removed from the boxes in which seeds were germinated, and seedling axial length was measured.

Seedlings were grouped according to those that were <2, 2–4, 4–6, 6–8, 8–10, or 10–15 mm in length. These seedlings were then placed in desiccators at 20% relative humidity and 24°C for 14 days. Relative humidity was controlled by filling desiccators with 350 ml of calcium chloride ($CaCl_2$) solution prepared according to Stokes (1949). Upon completion of the desiccation treatment, 3 blocks each containing 10 seedlings were selected, blotted dry on paper tissues and weighed. These seedlings were oven-dried at 80°C for 48 hours, weighed, and water content determined. Three more blocks of 20 seedlings for each seedling length group were rehydrated in 100 x 15 mm Petri dishes lined with 2 layers of No. 1 Whatman filter paper moistened with 4 ml distilled water, and incubated at 18°C in darkness for 7 days. Seedling survival was determined on the seventh day by examining root hair development; seedlings developing root hairs were considered live.

Reliability of using root hairs as the criterion of seedling survival in the following experiments was tested by randomly selecting seedlings from each seedling-length group, scoring root hairs, and transplanting them into 125 x 125 x 100 mm pots filled with wet 'Redi-earth' potting media. Seedling cotyledons were covered with about 5 mm of media. Pots were placed in a growth chamber at 15°C with light (220 µmol m^{-2} sec^{-1}) for 14 hours and 10°C darkness for 10 hours. Pots were watered every 2 days, and seedling survival was recorded after 21 days. Survival, judged by growth of root hairs provided a slightly high estimate of seedling emergence (Y = 7.8+0.93X where Y is seedling emergence from soil (%) and X is seedling survival (%) judged by the presence of root hairs, R^2 = 0.99, P <0.001).

Root hair development was used to assess seedling survival in Experiments II through IV. These experiments were repeated twice with 3 blocks per run in a randomized-complete-block design. Regression analyses were used to relate seedling survival and seedling length when desiccated with the best-fit model ($P \leq 0.05$) selected (Snedecor and Cochran 1980). Mid-points of seedling length classes were used as independent variables.

Experiment III—Effects of relative humidity on seedling survival

This experiment was conducted to test the hypothesis that relative humidity during desiccation affects seedling survival. Seeds were pretreated in a 600 mM ethanol solution and washed in water as in Experiment II. About 300 of these seeds were placed in 32 x 21 x 7 cm plastic boxes lined with 6 layers of germination paper wetted with 120 ml distilled water then incubated 4 days at 18°C in darkness. Seedlings were removed from the boxes, axial length measured, and seedlings were grouped into those that were 4-6 or 9-11 mm in length. Three blocks of 20 seedlings for each seedling-length group were placed in desiccators containing 350 ml $CaCl_2$ solution (Stokes 1949) prepared to create 30, 45, 60, 75, and 90% relative humidity. Calcium chloride powder, oven dried at 120°C for 48 hours, was used for 0% relative humidity. Desiccators were placed in an incubator at 25°C in darkness for 7 days. Upon completion of the desiccation treatment, 3 blocks each containing 10 seedlings were selected and weighed. These seedlings were oven-dried at 80°C for 48 hours, weighed, and water content determined.

This experiment was repeated twice with 3 blocks per run in a randomized-complete-block design. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Regression analyses were performed and best-fit models ($P \leq 0.05$) were selected (Snedecor and Cochran 1980) for untransformed data.

Experiment IV—Effects of varying lengths of desiccation on seedling survival

This experiment was conducted to test the hypothesis that the duration of desiccation affects seedling survival. Several hundred seeds were pretreated in ethanol and incubated as described in Experiment II. Twenty seedlings that were 7–10 mm long were desiccated at 20°C for 1, 4, 7, 10, 13, or 16 days over a $CaCl_2$ solution prepared to create 30% relative humidity. After the specified length of desiccation 20 seedlings were removed from the desiccator, rehydrated as in Experiment II, and incubated for 5 days at 18°C in darkness. On the fifth day, survival of seedlings for each desiccation treatment was determined.

Another lot of seeds was incubated as above, and on the fifth day seedlings were measured and grouped as being 2–5 or 7–10 mm long. These seedlings were desiccated in darkness for 7 days at 20°C in desiccators with $CaCl_2$ solutions prepared to create 30 or 90% relative humidity. Control was 100% relative humidity in sealed germination boxes with wet germination paper. Seedlings were removed from dessicators and germination boxes and placed in 100 x 15-mm Petri dishes lined with 2 layers of No.1 Whatman filter paper moistened with 4 ml distilled water. These seedlings were incubated at 18°C in darkness for 7 days and the lengths of 40 seedlings measured.

These tests, conducted in a randomized-complete-block with 3 blocks, were repeated twice. Relationships between days of desiccation and seedling survival were determined with regression analysis and the best-fit model ($P \leq 0.05$) was selected (Snedecor and Cochran 1980). In the second aspect of this study, analysis of variance was used, and means were separated with Least Significant Difference ($P \leq 0.05$).

Experiment V—Effects of desiccation on seedlings of different ages

Several hundred seeds were prepared and incubated in germination boxes as in Experiment I. One, 2, and 3 days after beginning incubation, seedlings that were 7–10 mm in length were removed from germination boxes and desiccated for 7 days at 25°C over $CaCl_2$ solutions prepared to create 30% relative humidity. Upon completion of the desiccation treatment, seedlings were rehydrated in 100 x 15-mm Petri dishes lined with 2 layers of No. 1 Whatman filter paper moistened with 4 ml distilled water, and incubated at 18°C in darkness for 7 days. Seedling survival was determined on the seventh day by examining root hair development; seedlings developing root hairs were considered live.

This experiment was repeated twice with 3 blocks per run in a randomized-complete-block design. Percentage data were transformed into arcsin angles and subjected to analysis of variance (Snedecor and Cochran 1980). Means were with separated with Least Significant Difference ($P<0.05$); untransformed data are presented.

Experiment VI—Effects of varying periods of desiccation and relative humidity on electrolyte leakage from seedlings

Seeds were pretreated with ethanol and germinated as described in Experiment II. Seedlings of <2, 4–6, or 9–11-mm lengths were placed in desiccators containing $CaCl_2$ solutions with 30 or 90% relative humidity at 20°C for 7 days. Control seedlings were placed in sealed germination boxes with wet germination paper to create 100% relative humidity. Three blocks, each containing 7 seedlings from each length category and humidity treatment, were soaked in 3 ml distilled water at room temperature. Electrical conductivity of the soaking solution was measured at 15, 30, 45, 60, 90, 120, 150, 180, 240, 300, 360, 420, or 480 minutes of soaking with a YSI Model 32 conductance meter. Three new blocks were used for each period of soaking. The number of seedlings and water volume were determined in preliminary experiments so measurements fell into the range of the instrument.

This experiment was repeated twice in a randomized-complete-block design with 3 blocks per run. Best-fit regression equations were selected ($P \leq 0.05$) (Snedecor and Cochran 1980) to describe relationships between soaking time and electrical conductivity for each size class of seedlings and relative humidity.

Results

Effects of hydration-desiccation cycles on seed germination and seedling growth

Initial seed water content was about 5%. Water content peaked at about 35% on the second hydration-desiccation cycle and decreased as the number of hydration-desiccation cycles increased from 2 to 10 (Y = 36.1–0.06X, where Y is water content (%) and X is the number of hydration-desiccation cycles; R^2 = 0.55, P$\leq$0.05). Water content of dehydrated seeds did not change after the first cycle and averaged 13.4% (SE = 0.4). When rehydrated for 24 hours after the hydration-desiccation cycles, water content of seeds averaged 141% (SE = 1.9).

Total germination percentage varied among hydration-desiccation cycles, but was not correlated (P>0.05) with the number of cycles and averaged 66% (SE = 1.5). Seeds germinated faster with exposure to increasing number of hydration-desiccation cycles (Y = 37.3 + 0.6X, where Y is germination rate (% day^{-1}) and X is the number of hydration-desiccation cycles, R^2 = 0.33, P$\leq$0.05). Of the seeds that did not germinate, seed decay increased about 1.5% with each hydration-desiccation cycle (Y = 16.2+1.5X, where Y is seed decay (% of seeds incubated), and X is the number of hydration-desiccation cycles, R^2 = 0.53, P$\leq$0.05). Axial length of seedlings increased with increasing number of hydration-desiccation cycles (Y = 34.7+0.05X, where Y is seedling axial length (mm) and X is the number of hydration-desiccation cycles, R^2 = 0.44, P$\leq$0.05).

Effects of desiccation on survival of different size seedlings

Seedling survival after 14 days of desiccation at 20% relative humidity declined as seedling length increased (Y = 113.9–10.04X where Y is seedling survival (%) X is seedling length (mm), R^2 = 0.90, P = 0.004). Final water content of desiccated seedlings ranged from 4.9 to 5.5%, but was not correlated (P>0.05) with survival.

Effects of relative humidity on seedling survival

Survival of desiccated seedlings 4-6 or 9-11 mm in length increased as relative humidity increased (Fig. 1). The difference in survival between 0 and 90% relative humidity was 62% for 4–6 mm seedlings and 70% for 9–11 mm ones. Survival of 4–6 mm seedlings was 20 to 45% higher than that of 9–11 mm seedlings after desiccation. As expected, water content of desiccated seedlings also increased with increasing relative humidity (Fig. 1). After desiccation at 75 and 90% relative humidity, 9–11 mm seedlings contained more water than those that were 4–6 mm long.

Effects of varying lengths of desiccation on seedling survival and growth

Seedling survival decreased curvilinearly as the length of desiccation increased from 1 to 16 days (Fig. 2). Seedling survival was about 67% for seedlings desiccated 1 day compared to 31% for those desiccated 16 days. Water content of desiccated seedlings was similar (P>0.05) after different lengths of desiccation, averaging 7.5% (SE = 1.1).

Desiccation at 30 and 90% relative humidity produced similar effects on growth of seedlings that survived, even though survival differed with relative humidity. Growth was reduced for 7–10 mm long seedlings that survived 7 days of desiccation, but growth of 2–5 mm long seedlings was not affected by desiccation (Fig. 3). Abnormal growth, twisted or sharply curved radicles, was observed among seedlings that survived desiccation.

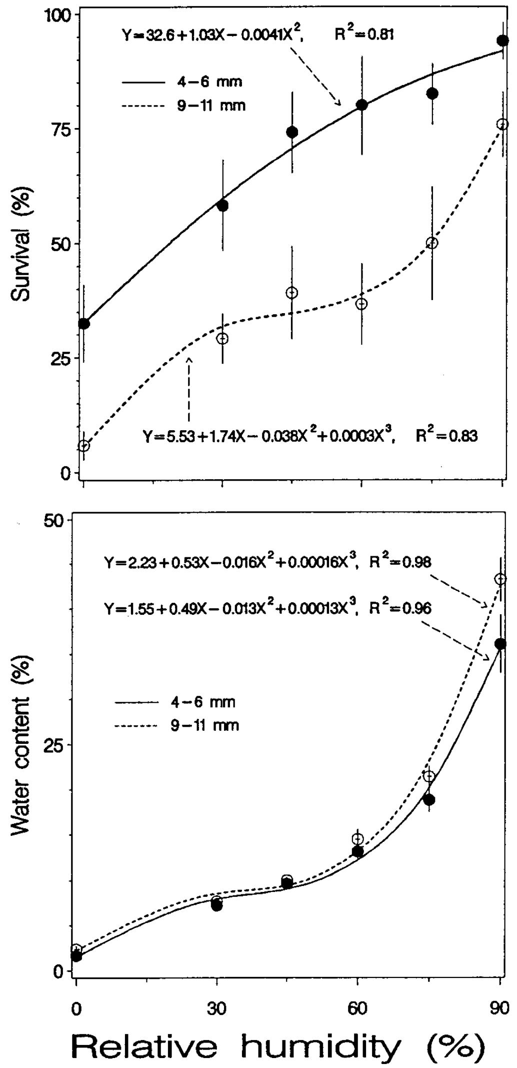

Fig. 1. Fitted regression lines for survival and water content in winterfat seedlings of 4–6 mm and 9–11 mm lengths after 7 days of desiccation at relative humidities between 0 and 90%. Each value is the mean±SE of 6 replicates of 20 seedlings. If no vertical bar is evident, SE is less than the size of the symbol.

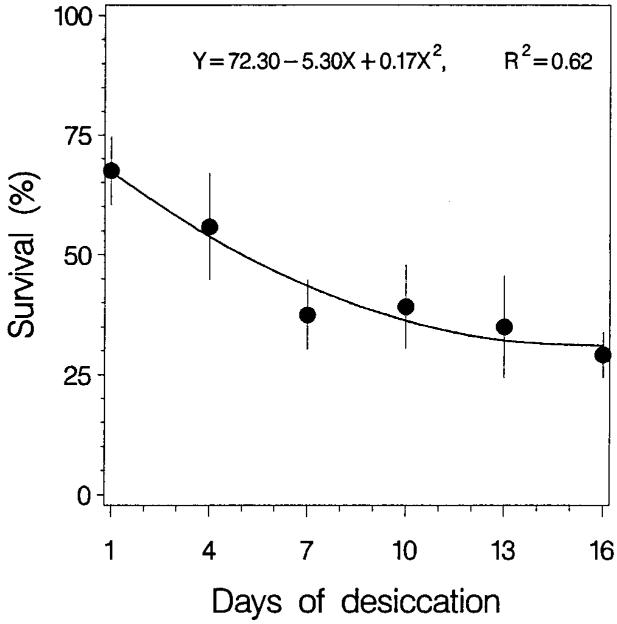

Fig. 2. Fitted regression lines for survival of 7–10 mm long winterfat seedlings after desiccation at 20°C and 30% relative humidity for 1 to 16 days. Each value is the mean±SE of 6 replicates of 20 seedlings.

Effects of desiccation on survival of seedlings of different ages

Survival of desiccated seedlings varied among times of seed germination. Desiccated seedlings from seeds germinating on the first day averaged 64% (SE±3.5) compared to 40% (SE±4.3), and 23% (SE±2.1) on the second and third days, respectively.

Effects of varying lengths of desiccation and relative humidity on electrolyte leakage from seedlings

Decreasing relative humidity and increasing seedling length contributed to greater electrolyte leakage from seedlings (Fig. 4, Table 1). Leakage increased faster at earlier than later stages of soaking.

Discussion

Seeds are generally tolerant of wetting and drying (Hegarty 1978, Hassanyar and Wilson 1979, Friedman et al. 1981, Hong and Ellis 1992). Lack of correlation between germination and number of hydration-desiccation cycles, as observed in this study, indicates that germination of viable winterfat seeds is not likely impaired or favored by repeated moisture fluctuations in the field. This response contrasts with forage kochia (*Kochia prostrata*) (Haferkamp et al. 1990) and spiny hopsage (*Grayia spinosa*) (Shaw et al. 1994) in which germination is increased by wetting and drying cycles under field conditions. Germination rate and seedling growth of winterfat actually increased after hydration-desiccation treatments, and may be attributed to the well-known effect of priming (Hegarty 1978). Germination rate of forage kochia and spiny hopsage also increases following periods of wetting and drying (Haferkamp et al. 1990, Shaw et al. 1994). Increased seed decay in ungerminated seeds after hydration-dehydration treatments suggests some seeds were damaged by wetting and drying, but this damage apparently did not affect germination during the test period. It could, however, be expected that such damage over prolonged periods of moisture fluctuations may eventually reduce the viable seed population, and hence germination of winterfat in the field. Booth et al. (1999) discovered significant deterioration of mitochondria in 6-month-old winterfat seeds at 20°C and 50% moisture, a relatively high water content for seeds. This deterioration did not occur at 5°C, and they attributed the deterioration at 20°C to a lack of translocation of food reserves within partially hydrated seeds with high respiration rates.

Survival and growth of winterfat seedlings can be negatively affected by desiccation, depending on seedling growth stage, and intensity and duration of desiccation. Tolerance and avoidance are mechanisms of resisting stress in

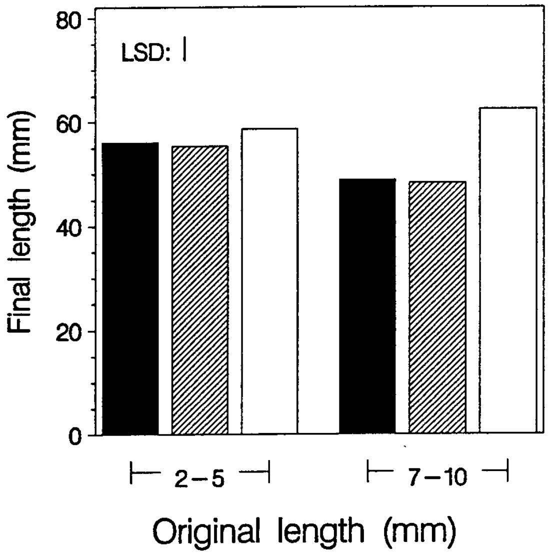

Fig. 3. Growth of winterfat seedlings that were 2–5 or 7–10 mm in length and survived 7 days of desiccation at 20°C, 30, 90, or 100% relative humidity. The final length was measured 7 days after rehydrating and incubating seedlings at 18°C in darkness. Desiccation treatments were 30 (solid bar) or 90% relative humidity (hatched bar), and control (empty bar) (100% relative humidity in sealed germination boxes). Each bar is the mean of 40 seedlings. LSD is least significant difference among means (P<0.05).

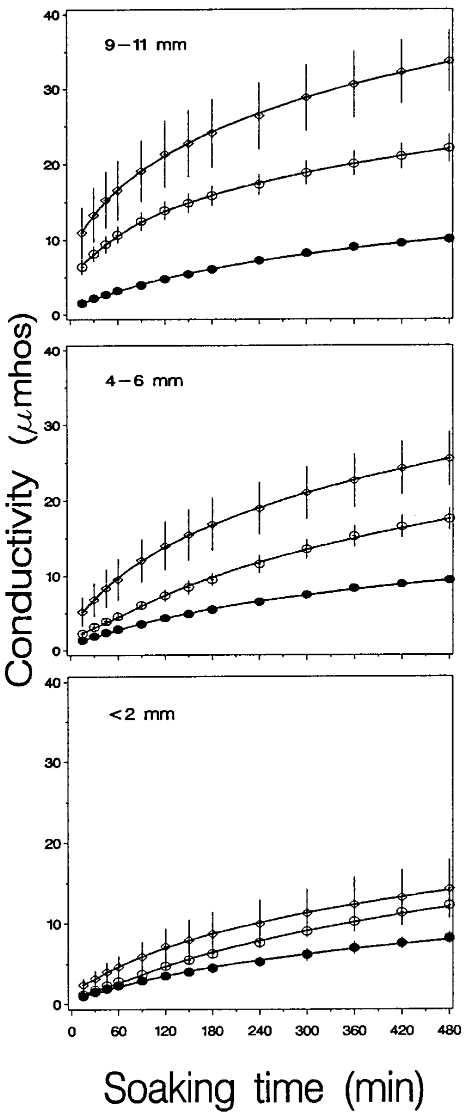

Fig. 4. Fitted regression lines for electrolyte leakage from winterfat seedlings of different lengths after desiccation at 30, 90, or 100% relative humidity. In each graph the upper, middle and lower lines are for desiccation at 100, 90 and 30% relative humidity, respectively. Each value is the mean±SE of 6 replicates. If no vertical bar is evident, SE is less than the size of the symbol. Regression equations are presented in Table 1.

plants (Levitt 1980). Results of this study indicate that desiccation tolerance in winterfat seedlings is high at early stages of growth and diminishes as growth progresses. Similar changes in desiccation tolerance were reported for *Agropyron desertorum* and *Psathyrostachys juncea* (Hassanyar and Wilson 1979), *Anastatica hierochuntia* (Friedman et al. 1981), *Glycine max* (Senaratna and McKersie 1983), *Hordeum vulgare*, and *Vigna radiata* (Hong and Ellis 1992). Electrolyte leakage measurements support the argument that collapse of enlarged cells, and membrane injury, are primary causes of increased sensitivity to desiccation (Senaratna and McKersie 1983). As soils dry, mortality of 1- to 4-day old seedlings of winterfat is high (Waddington and Shoop 1995). Thus, once desiccation tolerance is lost, winterfat seedlings must avoid stress if they are to survive. A wet seedbed for 2 days is needed for emergence and growth of winterfat seedlings that can survive subsequent drying conditions (Waddington and Shoop 1995). Germination near 0°C (Hilton 1941, Booth 1987, Bai et al. 1998a) may allow root growth before warm temperatures dry the soil surface. Winterfat seeds do not germinate in the fall in the northern reaches of northern mixed prairie; however, seeds shed during the previous fall, germinate at low temperatures in early spring (Hou and Romo 1997). Water content of the soil surface is usually high at this time (Evans and Young 1970, Booth 1992). Seedlings grow slowly at low temperatures (Hou and Romo 1997), and they may tolerate desiccation. Desiccation alone is not, therefore, likely to threaten survival of winterfat seedlings in early spring. It is possible, however, that radicles of seedlings may not be able to penetrate frozen soil, and seedlings may desiccate.

As temperatures increase and seedlings grow, their survival will be increasingly threatened by freezing temperatures (Hou and Romo 1997, Bai et al. 1998b) and desiccation. Litter or soil cover may increase seedling establishment because of high soil moisture retention (Evans and Young 1970, Springfield 1971, Fowler 1986, Cheplick and Quinn 1987). Evans and Young (1970) reported a diurnal range of relative humidity between 60 and 95% under plant litter in the field, compared to relative humidity below 30%

Table 1. Regression equations for electrolyte leakage from winterfat seedlings <2, 4–6, and 9–11 mm in length and desiccated at 30, 90, or 100% relative humidity at 20°C for 7 days. Y = electrical conductivity (μmhos), X = soaking time (15 to 480 minutes). Fitted curves are presented in Figure 4.

Seedling length	Relative humidity	Regression equation	R^2
(mm)	(%)		
<2	30	$Y= 7.48–4.15\ln X+0.85\ln X^2$	0.65
	90	$Y=11.00–6.42\ln X+1.07\ln X^2$	0.95
	100	$Y= 5.98–3.43\ln X+0.61\ln X^2$	0.93
4-6	30	$Y= 9.71–5.03\ln X+1.23\ln X^2$	0.78
	90	$Y=14.89–8.43\ln X+1.44\ln X^2$	0.96
	100	$Y= 6.46–3.65\ln X+0.67\ln X^2$	0.98
9-11	30	$Y=13.60–4.17\ln X+1.20\ln X^2$	0.70
	90	$Y= 5.84–1.65\ln X+0.69\ln X^2$	0.91
	100	$Y= 6.03–3.41\ln X+0.66\ln X^2$	0.97

during the day on bare soil. The current study indicates that chances of survival in winterfat can be substantially higher when relative humidity is within the range of 60 to 90%. Seedlings developing from seeds that germinate on, versus under litter (including diaspore aggregations), may not benefit from improved moisture conditions because they may not be exposed to high humidity and large amounts of litter can prevent radicles from reaching the soil (Fowler 1986, Booth 1987, Booth and Haferkamp 1995). Desiccation of winterfat seedlings with radicles exposed in air is detrimental, as demonstrated by 100% mortality in seedlings >10 mm in length. On the other hand, entry of the radicle into soil from diaspores on the surface may be favored by loose soil, high soil moisture, and increased heterogeneity of the soil surface (Campbell and Swain 1973). Diaspores may germinate during a 1- to 4-day period of high moisture (Waddington and Shoop 1995), but many seedlings will likely die if their roots do not reach a stable water supply.

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Book Reviews

Ecoregions. The Ecosystem Geography of Oceans and Continents. By Robert G. Bailey. 1998. Springer-Verlag Inc., New York. 176 p. $US79.95 cloth, $US39.95 paper. ISBN 0-387-98305-8 cloth, 0-387-98311-2 paper.

Flourishing interest in landscape ecology should ensure an audience for *Ecoregions*, a recent global survey of ecosystem geography. This semi-technical treatment follows by 3 years Bailey's *Ecosystem Geography* (reviewed in J. Range Manage., 49:479–480), which addressed many of the same matters on a more detailed, regional scale.

The 9 chapters constituting the text of the book are essentially a large-scale classification of ecosystem regions, or *ecoregions*, defined by Bailey in the introductory Chapter 1 as portions of the earth's surface over which the ecosystems have characteristics in common. Chapter 2 discusses the variables involved in determining and classifying large-scale oceanic types. It includes an hierarchical subdivision of the world's oceans into polar, temperate and tropical *domains*, and into smaller-scale *divisions*, based on the work of earlier researchers, but involving some variations by the author. These subdivisions are the basis of the global classification of oceanic regions in Chapter 3, in which the oceans are divided into subdivisions with names like the *High Salinity Subtropical Division*, and the *Outer Polar Division*. Chapter 4 is a terrestrial analog of Chapter 2, examining the variables such as latitude, elevation, and continental position involved in determining and classifying continental types. Again, the hierarchical classification of the continental types is based on the work of previous researchers, with some modifications by Dr. Bailey. Chapter 4 also includes a discussion of the Koppen-Trewartha classification of climates, and a discussion of the distribution and extent of the continental subdivisions.

Chapters 5–8 examine the different continental ecoregions, beginning with the polar ecoregions in Chapter 5. Most of the discussion here involves characteristics of arctic and subarctic divisions, with little on Anarctica, where, presumably, one finds little to subclassify, except perhaps other scientists. Chapter 6 focuses on the humid temperate ecoregions, including such *divisions* as the *Mediterranean*, and *Prairie*. The Dry Ecoregions, the subject of Chapter 7, involves many of the important rangeland divisions. The *Humid Tropical* and *Mountain Ecoregions* are combined into Chapter 8, and include divisions such as tropical savannas, and altitudinal spectra of types. The Summary and Conclusions of Chapter 9 fill only half a page. Three Appendices, on air masses and frontal zones, common and scientific names, and conversion factors, respectively, follow the text, and are themselves followed by a glossary of technical terms, a selected bibliography, a few notes about the author, and a detailed general index. Small but detailed color maps of *Ecoregions of the Oceans*, and *Ecoregions of the Continents* are included in a vinyl sleeve inside the back cover.

As is true of any book on classification, *Ecoregions* is all about scale. The proliferation of classifications, mainly applied to regional or local habitats in the 1960's and 1970's is, in the landscape conscious 1990's, seemingly being repeated, just as prolifically, on larger scales, with different jargon. Much of the basic ecology can be found in earlier books such as Walter's *Vegetation of the Earth*, and earlier landscape classifications can be found as well. The incremental technical merit of a book on classification such as *Ecoregions* can be judged partly on how effectively and how *consistently* the author uses the classification protocol he has laid out in his own book in his subsequent analyses in that book. Bailey's book is generally consistent in its usage of classification jargon, and more impressively, its text trots along easily, without excessive detail, so that while the discussions are rigorous, the syntax doesn't suffer from the structured, repetitive *rigor mortis* that has stiffened so many past writings on ecological classification. *Ecoregions* reads well.

It would hardly matter if it didn't. Considering that it is a semi-technical book written by a landscape ecologist, *Ecoregion's* graphics are slicker than the vinyl sleeve that holds the maps inside the back cover. An artful combination of colorful figures and maps, well-chosen color *and* black-and white photographs, including impressive aerial photographs, and even an original drawing, all combine in the kind of balanced, coherent, energetic, and seemingly spontaneous graphics display that only meticulous planning can produce. And of course, it all looks simple. A few of those funky mid-century souvenir postcards here and there from the author's personal collection even add a little *kitsch*. What fun.—*David L. Scarnecchia*, Washington State University, Pullman, Washington.

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