

Journal of Range Management

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Invited Paper

Stubble height as a tool for management of riparian areas

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Abstract

Stubble height, a measure of the herbaceous vegetation remaining after grazing, has been widely used in recent years to gauge the impacts of grazing use in riparian areas. Stubble height is a short-term management guide that should only be applied to help attain long-term ecological objectives; it should not be thought of as a long-term management objective.

Maintaining a minimum stubble height helps preserve forage plant vigor, retain sufficient forage to reduce cattle browsing of willows (*Salix* spp.), stabilize sediments, indirectly limit stream-bank trampling, maintain cattle gains, and provide an easily communicated management criterion. Based on limited specific research of riparian system response and on knowledge of the characteristics of how cattle graze, a 10-cm residual stubble height is recommended by the authors as a starting point for improved riparian grazing management. Monitoring should then be conducted to determine if an adjustment is needed. In some situations, 7 cm or even less stubble height may provide for adequate riparian ecosystem function, particularly when stream-banks are dry and stable or possibly at high elevations where vegetation is naturally of low stature. In other situations, 15–20 cm of stubble height may be required to reduce browsing of willows or limit trampling impact to vulnerable streambanks. The recommended criterion would apply to streamside and nearby meadow sites with hydrophilic or potentially hydrophilic vegetation, but not directly to dry meadows or even to all wet meadows. Stubble height may have little application where the stream-banks are stabilized by coarse substrates, or the channels are deeply incised.

The effects of residual stubble height in riparian functions have received limited direct experimental examination. Consequently, much of the information in this review was derived from studies indirectly related to the questions raised and, to some extent, from observations of experienced professionals. The authors have identified areas of scientific investigation needed to improve our understanding of the effects of stubble height on riparian function and grazing management.

Key Words: Grazing, livestock management, streambanks, trampling, utilization, willow

In the early settlement history of the western United States management of riparian grazing lands was pretty straightforward—no irrigation or stock water to worry about—just turn the

Resumen

La altura del rastrojo, una medida de la vegetación herbácea remanente después de que ha sido sujeta a apacentamiento, ha sido ampliamente utilizada en años recientes para medir el impacto del apacentamiento en las áreas ribereñas. La altura del rastrojo es una guía de manejo a corto plazo que debe ser aplicada solo para ayudar a lograr los objetivos ecológicos de largo plazo y no debe ser tomada como un objetivo de manejo a largo plazo.

El mantener una altura mínima del rastrojo ayuda a preservar el vigor de las plantas forrajeras, retener suficiente forraje para reducir el ramoneo de “Willows” (*Salix* spp.) por el ganado, estabilizar los sedimentos e indirectamente limitar el pisoteo del banco de la corriente, mantener las ganancias del ganado y proveer un criterio de manejo fácilmente comunicable. Basado en la escasa investigación específica sobre la respuesta de los sistemas ribereños y en el conocimiento de como el ganado apacienta, se recomienda una altura del rastrojo de 10 cm como el punto inicial para el manejo del apacentamiento que mejore las áreas ribereñas. El monitoreo debe entonces ser conducido para determinar si es necesario un ajuste. En algunas situaciones 7 o menos centímetros de altura del rastrojo pueden ser suficientes para el buen funcionamiento del sistema ribereño, particularmente cuando el banco de la corriente está seco y estable o posiblemente en elevaciones altas donde la vegetación por naturaleza es de porte bajo. En otras situaciones 15 a 20 cm pueden ser requeridos para reducir el ramoneo de “Willows” o limitar el impacto del pisoteo en los bancos de corriente vulnerables. El criterio recomendado aplicaría a las playas y vegas cercanas con vegetación hidrofóbica o potencialmente hidrofóbica, pero no directamente a las vegas secas o no a todas las vegas húmedas. La altura del rastrojo puede tener poca aplicación donde el banco de la corriente está estabilizado por estratos gruesos o los canales de incisión profunda.

Los efectos de la altura del rastrojo residual en las funciones ribereñas ha recibido poca atención experimental directa. Consecuentemente, mucha información de esta revisión se derivó de estudio relacionados indirectamente a las preguntas surgidas y en parte también de observaciones de profesionales experimentados. Los autores han identificado áreas de investigación científica necesarias para mejorar nuestro entendimiento de los efectos de la altura del rastrojo en las funciones de ribereñas y manejo del apacentamiento.

livestock out in the spring and take them home in the fall. We now know that proper management of these highly diverse ecosystems is not that easy. These land-water ecotones are among the most ecologically productive and diverse of all terrestrial habitats, and the influence of moving water within stream riparian

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an zones often results in rapid and dynamic habitat changes (Naiman et al. 1993).

As society's interest in public land has increased, interest in riparian grazing management issues has increased as well (US GAO 1988, Belsky et al. 1999). Many managers are currently using residual herbaceous stubble height in the riparian zone as a measure of the vegetation remaining after grazing. Stubble height has also been suggested as a gage to various impacts of grazing use (Skinner 1998). In this paper we present what is known about stubble height and its use as a tool for managing riparian areas.

Historical Perspective

Stubble height standards were used earlier in this century to guide the grazing management of rangelands, particularly those in the Southwest (Crafts 1937, Parker 1942). Several range scientists developed techniques for determining stubble height (Reid and Pickford 1941, Canfield 1942a, 1942b, 1944). Guidelines were specific to each forage species and generally crafted to approximate a utilization level determined at the end of the grazing season or year. In some instances, stubble height standards were presented for different seasons of the year (Crafts 1937).

Textbooks continued to present stubble height and height-weight relationships as part of vegetation measurements through the 1980s (Brown 1954, Cook and Stubbendieck 1986, Bonham 1989), often as a method to estimate utilization (Stoddard et al. 1975, Holechek et al. 1989). However, field use of stubble height seemed to give way to direct estimates of utilization percentages (Sanders 1998). Use of utilization per se as a management tool has been questioned (Frost et al. 1994, Sharp et al. 1994, and by several participants at a workshop [OSU, AES 1998]). A broad contention was that utilization measures are flawed because of irregular consumption within and between plants, mismatching of utilization standards and plant phenology, problems in determination of actual utilization levels, and confusion of management tools with management objectives (OSU-AES 1998). Similar issues can be raised for the use of stubble height as a grazing management tool.

Various researchers have focused on residual vegetation as the important element in grazing management. A number of residual vegetation recommendations have been developed through research and

experience. For example, herbage production was maintained and maximum financial returns from livestock grazing were achieved when approximately 340 kg ha⁻¹ of residue was preserved on shortgrass prairie in eastern Colorado (Bement 1969). In California the residue needed to maintain an adequate mulch layer and soil organic matter to support mountain meadow stability varied from 110 to 3,200 kg ha⁻¹ depending upon meadow condition and elevation (Ratliff et al. 1987). Maintenance of minimum residue amounts has been recommended to maintain herbivore productivity (Heady and Child 1994). Approximate residual biomass can be estimated from height-weight relationships and stubble heights (Ratliff et al. 1987, Mitchell et al. 1993, Heady and Child 1994, Leonard et al. 1997).

Some people have stated that stubble height may possibly be easier to visualize, measure, and communicate than is residual weight of forage or estimates of percentage utilization (Canfield 1942a, USDI-BLM 1996, Leonard et al. 1997). Others have objected to the general application of stubble height or other utilization standards as not appropriate for all situations (Chaney et al. 1993, George 1996).

A determination of current livestock use does appear to be important for most management situations. Holechek et al. (1998, 1999), after reviewing numerous grazing studies, concluded that stocking rate rather than the grazing system was the primary factor that affected range condition and financial returns. Forage utilization (expression of forage removed) and residual vegetation (expression of forage remaining) both provide some measure of comparative stocking rates.

How Are Riparian Areas Different From Adjacent Uplands?

Riparian ecosystems occur along the edges of water bodies, but are usually associated with streams. Although vegetation is often the most conspicuous part of a riparian ecosystem, the entire system comprises a variety of life forms and abiotic environmental features (Kauffman and Krueger 1984). Unbound water either directly or indirectly influences all of the functional and structural characteristics of these zones (Hawkins 1994). Riparian ecosystems are of great interest because, although ecologically connected, they are usually functionally and structurally unique from adjacent upland systems. Near-stream environments are hydrologi-

cally and geomorphically dynamic in that periodic flooding typically scours channel and flood plain surfaces in some areas and deposits material in others. These natural disturbances form the complex habitats found in riparian systems (Hawkins 1994, Swanson 1994). Unfortunately, the disturbance and successional patterns of riparian areas are highly vulnerable to influence by human activities that are often concentrated in water-influenced areas (Groeneveld and Or 1994, Busch and Scott 1995). Such activities include grazing, recreation, logging, mining, water diversion, agriculture, and road construction.

A major function of riparian-stream systems is to provide routing or transfer of water, energy, sediment, nutrients, particulate organic matter, and organisms (Odum 1978, Gregory et al. 1991, Johnston 1993, Risser 1995). Such transfers are not only in a down stream direction, but may move laterally, sometimes being deposited onto flood plains and at other times moving materials from the land into the stream (Gregory et al. 1991, Kattlemann and Embury 1996). The biogeochemical cycles of riparian areas differ from surrounding uplands or adjacent dry meadows (Green and Kauffman 1989). Wet soil conditions in streamside riparian areas often result in anaerobic situations, at least during the earlier portion of the growing season. Anaerobic biochemical reactions serve to alter the state of elements in water passing through them prior to entering streams and lakes. Under anaerobic conditions, microbial processes help produce reduced forms of elements such as carbon, nitrogen, and sulphur that can be released into the atmosphere (Hussey et al. 1985, Schlesinger 1991, Hill 1996, Schnabel et al. 1996). Riparian areas can serve as a sink for phosphorus-laden sediments, further upgrading water quality (Green and Kauffman 1989, Corley et al. 1999). The presence of herbaceous vegetation improves water quality by enhancing sediment deposition. This process often facilitates the channel restoration process particularly in small-stream (e.g., ~5 m width or less) systems (Hawkins 1994, Clary et al. 1996, Pearce et al. 1998a).

In most of the western United States, the interface of stream-riparian areas with the more arid uplands creates the ultimate in dynamic ecotones. The upland-riparian-aquatic mosaic composes an amazing platform for biotic diversity (Fitch and Adams 1998). The ecotonal nature of riparian areas with their high productivity and variety often supports a highly diverse biota represented by species from adjacent upland and

aquatic environments, as well as species unique to the riparian area (Odum 1978, Thomas et al. 1979, Kauffman et al. 1985, Larson 1993, Logan 1997).

Cattle congregate on meadows and riparian areas. They favor riparian area forage and water availability, topography, and general lack of physical constraints to grazing as compared to the drier and often rougher characteristics of upland areas (Reid and Pickford 1946, Roath and Krueger 1982b, Pinchak et al. 1991). This leads to particular concern toward grazing impacts (Chaney et al. 1993, Belsky et al. 1999). Because of moving water's erosive energy, maintaining hydrophilic herbaceous and woody plants is extremely important in many riparian situations (Beschta and Platts 1986, Manning et al. 1989, Gregory et al. 1991, Dunaway et al. 1994). If heavily rooted hydrophilic plants such as Nebraska sedge (*Carex nebrascensis* Dewey) and Baltic rush (*Juncus balticus* Willd.) are replaced by species with less root biomass and root length, streambank instability and channel lateral expansion often occur. This can result in a lowering of the local flood plain water table (Winward 1994). An example of such a species is Kentucky bluegrass (*Poa pratensis* L.), which is widespread on riparian areas where cattle graze heavily and channels are dynamic (Skinner 1998). Its comparatively limited total root lengths provide less streambank protection than species such as Nebraska sedge and beaked sedge (*Carex utriculata* Booth, formerly *C. rostrata* Stokes) (Platts and Nelson 1989, Kleinfelder et al. 1992, Hansen et al. 1995). It should be noted, however, many non-meadow stream segments are stabilized by large substrate particles (Rosgen 1996) and are relatively insensitive to the effects of herbaceous composition or livestock use.

A strikingly important function of riparian areas is their contribution to the quality of stream fisheries habitat. Major concerns about the impacts of riparian grazing on fisheries habitats have been raised in recent decades (Armour et al. 1994). Stream channel profile, streambank stability, streamside vegetation, channel bottom embeddedness, stream sediments, and stream temperature are all critical fisheries habitat characteristics that can be directly or indirectly affected by livestock grazing practices (Meehan et al. 1977, Stuber 1985, Bjornn and Reiser 1991, Murphy and Meehan 1991).

Can forage stubble height be of more value as a management tool for riparian areas than on uplands? This may be so,

because of the dynamic, multi-dimensional nature of riparian areas. On upland areas forage plant vigor, production, reproduction, and survival, together with soil loss, have been the primary range management concerns (Stoddart et al. 1975, Pieper 1994). Land managers must consider these plus many water-driven factors when managing riparian areas (Winward 1994). Forage stubble height can serve as a surrogate for a variety of management impacts (Skinner 1998). Some of the potential effects of leaving residual stubble height are direct, while others are indirect. Both of these kinds of effects are discussed.

Effects of Using Stubble Height as a Riparian Management Tool

Direct effects

Streambank protection and sediment entrapment

The ability of vegetation, particularly herbaceous vegetation, to protect stream channels and waterways has been intensively studied since the mid 1900s. Engineers and agronomists worked together to determine the effects of species, stem length, stem density, stem stiffness, and channel characteristics on channel protection and flow resistance (Ree and Palmer 1949, Temple 1982, Masterman and Thorne 1992). In the northeastern United States, streambank vegetation appeared to change the roughness of the channel and shear strength of the substrate and to directly influence the shaping of channel dimensions. The channel form of small streams (peak flow of 0.6 to 2.8 m³ sec⁻¹) was found to be greatly influenced by whether the streamside vegetation was trees or herbaceous sod. A narrowing of streams with sodded banks was particularly evident (Zimmerman et al. 1967).

Observations of riparian areas in the western United States have suggested that the type of sod is very important in determining streambank stability. For example, streambanks dominated by Kentucky bluegrass communities appeared to have substantially less stability than those dominated by sedge (*Carex* spp.) (Platts and Nelson 1989). The root length density of species such as Nebraska sedge may be over 10 times greater and root mass may be over 6 times greater than for a species such as Nevada bluegrass (*Poa nevadensis* Vasey) (Manning et al. 1989). The benefits of greater root length density and root mass in alluvial meadow streambanks include greater resistance to particle ero-

sion and greater resistance to compression and shear (Kleinfelder et al. 1992, Dunaway et al. 1994). Foliage and stem length is also an important factor in protecting streambanks. As streamside vegetation is immersed under rising streamflows and the foliage is laid over from the force of the flow, the longer vegetation length provides the greater protection to the substrate surface (Clary et al. 1996, Skinner 1998).

A key element for restoring degraded stream channels is entrapping and retaining of sediment on or below bank top (Clary et al. 1996). The possibility of forage plant stubble heights directly affecting the potential deposition and retention of sediments was examined in a hydraulics laboratory setting. The amount of sediment entrapped in the channel was a function of the flow and the vegetation blade length. Blades of Kentucky bluegrass of less than 8 cm appeared to enhance sediment deposition, while 20-cm blades retained a greater percentage of the initial sediment deposits (Abt et al. 1994). Alternatively, the more rigid but less dense vegetation entrapped less sediment (Thornton et al. 1997). Overall, these laboratory studies suggested that short-to-mid length (1–15, or possibly as much as 20 cm) flexible vegetation may be the most effective in supporting the bank building process within a single sedimentation event (Clary et al. 1996, Thornton et al. 1997). Limited experimental data suggest that longer stubble heights (20 to 30 cm) will be similarly effective under multiple sedimentation events (Clary et al. 1996). The presence of vegetation with 1.3 cm of stubble height or greater stabilized 200–700% more sediment than non-vegetated conditions in laboratory studies (Thornton et al. 1995).

Field tests of the impact of stubble height on sediment deposition and retention, subject to the variability and interactions of the real world, have not shown definitive results. A field test of sediment deposition during winter/spring flow events in 4 natural streams was investigated in Nevada. Four residual vegetation heights (0, 5, 10 cm and unclipped [~ 30 cm]) were tested. There were no differences the first year of the study, but in the second year the 5-cm height often captured significantly more sediment than the other treatments (Bell 1998). Another test of sediment deposition under natural flow was conducted in Wyoming. No significant difference was noted among effects of 0, 1, 8, and 15 cm stubble heights in the first 2 years of relatively low sediment

deposition (Rumsey 1996 as cited in Skinner 1998). During following years of repeated and strong floods, the 8 and 15 cm stubble heights appeared to stabilize the greatest amount of sediment (Skinner 1998). Sediment deposition during overland flow was examined in Colorado and Wyoming using a rotating boom rainfall simulator in both the field and in the laboratory. No significant differences were found in runoff characteristics or sediment deposition related to stubble height under conditions of shallow, overland flow (Pearce et al. 1997; 1998a, 1998b; Frasier et al. 1998).

Although sufficient evidence is available to conclude that stubble height has some affect on sediment deposition and retention when the plants are inundated, a complex of factors influence sediment movement and deposition (Pearce et al. 1998b). Skinner (1998) suggested that grazing of vegetation may not be a significant consideration in sediment deposition compared to the effects of channel and streamflow attributes. Several examples of minimum initial vegetation impact are deposits on point bars and on floodplains. On point bars sediments are deposited to a substantial degree by helical flow of the stream meander. This does not require the presence of vegetation, but vegetation will stabilize the deposited material allowing the vertical development of the point bars (Morisawa 1968, Abt et al. 1994). Deposits on floodplains can also occur in the absence of vegetation as the spreading water slows and loses competence (Morisawa 1968). Again, the presence of vegetation is important for long-term stabilization of these deposits.

Forage plant vigor and regrowth

The effect of defoliation on growth and vigor of forage plants has been a focus of concern throughout the history of range management (Jameson 1963, Bedunah and Sosebee 1995), but little experimental knowledge has been developed on responses of riparian species to defoliation. Most available information is based on observation and professional experience (USDA-FS 1988, Hansen et al. 1995). Generally, it is assumed that riparian forage species can be grazed more intensively than upland species because of higher soil moisture and their surmised regrowth potential (Skinner 1998).

In the Spring Creek study in Wyoming, treatments of weekly to biweekly defoliations to 1, 8, and 15 cm for 4 years resulted in less biomass for clipped plants as compared with untreated controls,

Table 1. Nebraska sedge stubble heights, Sheep Creek, Colo.

	Percent removal of current standing crop		
	30% (Light)	60% (Medium)	90% (Heavy)
	(cm)		
Spring~25 May Shoot height~8 cm Stubble height	3.8	2.0	0.5
Early summer~27 June Shoot height~20 cm Stubble height	7.0	4.5	1.8
Late summer~5 August Shoot height~25 cm Stubble height	10.0	6.5	2.8
Fall~1 October Shoot height~30 cm Stubble height	15.0	9.0	3.5

although plants clipped at 1 cm produced more than did plants from the other 2 clipping treatments (Skinner 1998). In a study at Sheep Creek, Colo., Nebraska sedge was subjected to light, medium, and heavy defoliation during either spring, early-summer, late-summer, or fall for 3 years. Additional treatments included medium defoliation during each of the aforementioned periods (i.e., continuous use treatment) and an untreated control (Table 1). Light and medium defoliations once each year for 3 years appeared to have had little effect on Nebraska sedge leaf lengths, however, heavy defoliation treatments resulted in reductions in leaf growth the following June. Reduction of stubble height to 2.8 cm in late summer was particularly detrimental to leaf growth (Lamman 1994).

A grazing simulation plot-study conducted in Idaho and Oregon included the components of defoliation, compaction (or trampling), and sometimes, nutrient return. The simulations suggested that creeping bentgrass (*Agrostis stolonifera* L.) communities would tolerate grazing to a 5-cm level. However, a reduction in the following year's growth was noted in higher elevation sedge-dominated communities when they were grazed to a 5-cm height in the spring, or to a 10-cm height in late summer (Clary 1995).

One reason for differences in the apparent sensitivity of riparian plants to grazing, noted above as compared to defoliation studies cited in the literature, was the consideration of livestock compaction or trampling effects. In the Idaho-Oregon study, the reduction in height growth and biomass production was more consistently related with compaction (or perhaps trampling) than with defoliation (Clary 1995). The simulation of grazing by defoliation alone

does not account for physical impacts to plants caused by the grazing animals (Skinner 1998). The compaction or trampling effect on plant growth may often be due to a direct impact on the plants themselves rather than soil compaction as such because bulk densities of riparian soils often recover quickly during the freeze-thaw cycles of winter (Wheeler 1998, Q.D. Skinner, personal communication).

Managers often depend upon substantial regrowth in riparian plants, such as when grazing is removed at least 1 month before frost (Myers 1989), to attain protective plant cover for the over-winter period. This response, however, is not consistent. For example, lower elevation sites that support disturbance species such as Kentucky bluegrass or creeping bentgrass (redtop) may respond with substantial regrowth following summer grazing (W. Clary, unpublished data). However, higher elevation sites, particularly those that support substantial amounts of sedges and rushes (*Juncus* spp.), may have less than 5% regrowth in total standing crop during August and September (Sheeter and Svejcar 1997), or only 2.5 to 5 cm in average additional height (W. Clary, unpublished data). Gillen et al. (1985) recorded no regrowth after July in the Blue Mountains of Oregon. Therefore, it is concluded that for some areas meaningful increases in stubble height following grazing can not be assumed, particularly at higher elevations.

Indirect effects

Streambank trampling

Grazing animals affect rangelands in many ways in addition to defoliating plants (Laycock and Harniss 1974, Skinner 1998). The general effects of soil compaction by large herbivores have been

known for years (Alderfer and Robinson 1949, Lull 1959). Observers experienced in stream and riparian ecology have long noted problems of physical breakdown of streambanks when substantial livestock use occurred (Platts 1991). Heavy use by cattle can destabilize and break down streambanks as vegetation is weakened and the physical forces of hoof impacts shear off bank segments (Marlow and Pogacnik 1985, Trimble and Mendel 1995), although little specific information is available on the rates of livestock occupancy that result in measurable damage. Buckhouse et al. (1981) reported no increase in streambank erosion with moderate levels of livestock grazing, and Marlow and Pogacnik (1985) found that limiting livestock grazing to periods when streambanks were relatively dry could greatly reduce physical damage. In Idaho maintaining stubble heights of 10 to 14 cm allowed streambank recovery, although at a slower rate than occurred under no grazing (Clary 1999). Simulated grazing procedures have illustrated that relatively continuous hoof action can severely break down streambanks, while more restricted use can result in minimal changes (Clary and Kinney 2000).

We are not aware of studies that document the relationship between texture of substrate material and effectiveness of stubble height as a riparian management tool. Experiences of various people suggest that use of stubble height as a primary management guide is limited if streambank composition is fine textured and moist during the grazing period, and if it is particularly vulnerable to hoof shear. In those cases, streambank disturbance may have to be monitored directly or grazing may have to be limited to periods when the streambanks are dry (Chaney et al. 1993, D. Dallas, C. Marlow, and S. Smith, personal communications).

The relative preference for plant communities will change during the grazing period because of changing levels of forage availability and quality among sites and community types (Korpela 1992). Although cattle are generally more attracted to moist riparian areas than to drier uplands, grazing in the early part of the growing season often results in livestock concentrating their use on the drier, and often more grass-dominated, portions of the meadow or surrounding landscape (Marlow and Pogacnik 1986, Kovalchik 1987, Korpela 1992, Clary and Booth 1993, Hall and Bryant 1995, Huber et al. 1995, Krueger 1996). Other things being equal for a grazed site, the taller stands

will be selected first because bite mass and instantaneous intake rates are higher in taller stands (Laca et al. 1994, Demment et al. 1995, Distel et al. 1995). Cattle intake and preferences can be affected when forage stubble heights are reduced to about 7–10 cm (Ungar et al. 1991, Hall and Bryant 1995). At that point, cattle often shift their grazing use to plant communities initially considered less desirable to maintain needed intake levels (Korpela 1992, Bailey et al. 1996). As forage supplies are consumed in the uplands and dry meadows, livestock will move to locations where supplies are greater (Stuth 1991). In some instances, palatability and digestibility or comfort concerns may temporarily override forage height and abundance issues (Hodgson and Wilkinson 1968, Kinney and Clary 1998), but eventually the animals will move to feeding stations where they can maintain needed intake rates (Bailey et al. 1996). Cattle will increase their use of hydrophilic vegetation near the stream edge as stubble heights on the adjacent dry meadows become short and intake is reduced. However, there will be less impetus for the animals to shift to wet streamside areas if adequate feed intake can be maintained on drier locations.

Phenology is an important factor in distribution of grazing between riparian and upland areas. When forage matures and digestibility decreases, forage intake declines even though adequate forage is available (Redmon et al. 1995). Differential plant drying and maturation between riparian and adjacent areas can result in cattle shifting feeding stations to riparian areas, although there still could be adequate forage available on adjacent drier areas (Hall and Bryant 1995). Thus, appropriate upland stubble heights, as a guide to management, can potentially vary throughout the season because as upland forages mature greater stubble heights and stand biomass may be necessary to retain livestock grazing activity.

Livestock movement rates increase as the animals attempt to maintain forage intake as stand heights decrease and, therefore, bite weight and the intake rate decrease (Johnstone-Wallace and Kennedy 1944, Wright et al. 1990, Demment et al. 1995, Bailey et al. 1996). This increased movement and trailing can result in substantially more compaction and trampling damage to streambanks (USDA-FS and USDI-BLM 1993). Skinner (1998) suggested that plant stubble heights of both wet streamside areas and adjacent dry meadow or terrace areas could be used to

manage when livestock activity along streambanks may increase to a point where bank breakdown might occur more frequently. No specific guidelines were suggested.

Browsing of riparian shrubs

Ungulate grazing strategies for riparian areas can be successful if they integrate animal behavior, forage palatability, plant physiology, plant community responses, hydrology, and physical site characteristics (Krueger 1996). As part of this complex consideration, experienced observers have suggested that substantial grazing of willows (*Salix* spp.) and other important riparian shrubs usually does not occur if a sufficient herbaceous forage supply is present, particularly if the forage is lush and palatable (Roath and Krueger 1982a, Kauffman et al. 1983, Mosley et al. 1997). Conversely, when herbaceous forage is in short supply or has matured, increases in willow consumption by cattle are expected (Hall and Bryant 1995, Skinner 1998). Hall and Bryant (1995) estimated that little use of riparian shrubs will occur if at least 7.6 cm of herbaceous stubble height remains. Observations by Kovalchik and Elmore (1992) suggest that mid to late season shrub use would begin at about 10 to 15 cm of forage stubble height, and browsing would continue to increase until cattle would browse all the willows they could reach when herbaceous stubble heights were reduced to less than 5 cm in height. It is unclear, however, how stubble height interacts with forage preference when the forage species are highly preferred, but of low stature. Anecdotal accounts vary on this issue.

A study specifically directed toward answering the question of the effect of residual forage on grazing use of willows was conducted in Colorado. The effects of season of use and that of residual forage stubble height on the proportion of willows in steer diets were separated through the use of a series of grazing paddocks. Results showed that some willow was consumed throughout the grazing season, but large increases in consumption occurred during the fall grazing period and anytime herbaceous stubble heights were short (Pelster 1998). Generally, willow consumption increased as forage stubble heights decreased to 15 cm in spring and early summer, while about 20 cm of stubble was needed to reduce willow consumption in late summer and fall. These findings, from a productive site (~3200 kg ha⁻¹ of herbage) dominated by water sedge (*Carex aquatilis* Wahl.) and beaked sedge, indicated a greater stubble height (i.e., more conserva-

tive management) might be required to adequately protect the willow community than was previously realized, at least in willow/tall sedge communities (Fig. 1).

Livestock gains

High daily gain is the keystone of effective livestock production. Maintenance of high rates of forage intake is necessary to accomplish this objective. Various factors affect rates of intake. The intake rate of foraging livestock is greatest in areas of abundant, palatable forage (Stuth 1991, Bailey et al. 1996). When the quantity of forage available is adequate, intake may be regulated by forage digestibility (Hodgson and Wilkinson 1968, Huston and Pinchak 1991, Redmon et al. 1995). Otherwise, the total mass of forage available directly affects intake rates (Johnstone-Wallace and Kennedy 1944, Handl and Rittenhouse 1972, Hobbs et al. 1996). Numerous studies have shown that bite depth, bite volume, intake rate, and total intake are related to the height of the forage stand (i.e., stubble height) (Allden and Whittaker 1970, Chacon and Stobbs 1976, Burlison et al. 1991, Laca et al. 1992, Laca et al. 1994). When the forage supply is largely consumed, bite size decreases and there is a markedly lower intake of herbage as compared to when stand heights are greater.

Stubble heights of 10 cm or less are often related to significant depressions in forage intake by cattle (Ungar et al. 1991). Cattle are bulk roughage grazers that use a tongue sweep to aid in forage ingestion (Huston and Pinchak 1991). The effectiveness of the tongue sweep is greatly reduced when forage heights are short, which contributes to reduction in bite volume (Ungar et al. 1991, Hall and Bryant 1995). Cattle may be reluctant to graze forage stands of only 4 cm in height (Ungar et al. 1991). For example, if 50% of the biomass of tufted hairgrass (*Deschampsia cespitosa* (L.) Beauv.) is removed, only about 4 cm of stubble height will remain (Kinney and Clary 1994), well below the optimum foraging lengths. Thus, even though tufted hairgrass is a preferred forage species (Clary and Booth 1993), a switch to other taller community-types may occur quickly if animals are to maintain dietary intake.

Measurement and communication

Sampling of stubble height can be relatively simple compared with many other vegetation measurements, or somewhat difficult depending on stand characteristics. Upland bunchgrass stands often are grazed

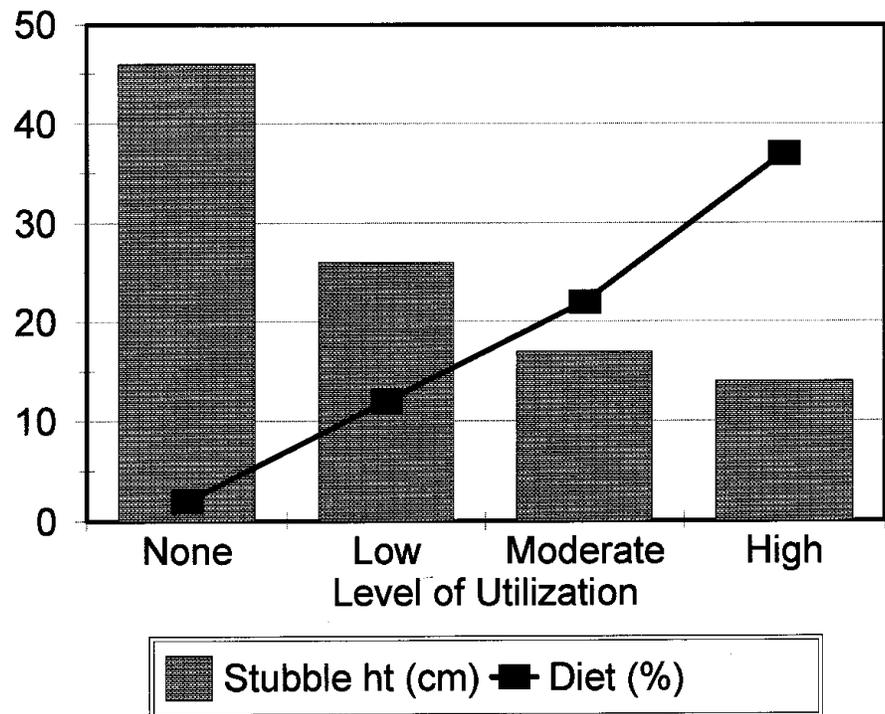


Fig. 1. Proportion of willow biomass in steer diets at different residual forage stubble heights. Data presented are average values for all stubble height levels from spring through fall, Sheep Creek, Colo. (after Pelster 1998).

irregularly, which makes interpretation of stubble height a problem (McKinney 1997). Alternatively, in more uniform or sod-like stands, grazing animals tend to remove the forage by horizons or levels (Laca et al. 1994). Sod-like stands of comparatively consistent plant composition often occur in riparian meadows within uniform soil moisture strata. This characteristic allows stubble height to be a more easily sampled variable on riparian areas than on many other rangelands.

Average riparian stubble height is typically determined by transects along the streamside area (K. Crane, personal communication). However, stubble height distributions in riparian areas, even though more uniform than on many upland sites, are often skewed with a portion of tall heights causing the average stubble height to be greater than other measures of central tendency (Gibb and Ridout 1988, D. Blackstun personal communication). The Bureau of Land Management has prepared a photographic guide to aid managers in rapidly judging median stubble heights (USDI-BLM 1999). Another rapid sampling approach for stubble height uses sequential sampling of plots recorded as meeting or not meeting a stubble height standard. This method has the advantages of avoiding the skewness issue, being rapid, and providing statistically defend-

able answers (Turner and Clary 2001).

The comparative ease of sampling stubble height aids in the manager-user communication process. Easily understood and communicated management goals are necessary, particularly when public lands are involved. While vegetation successional stage and trend are generally the appropriate long-term management goals, short-term objectives or guidelines are also necessary to help attain the long-term goals (Leonard et al. 1997). Forage utilization has been long used as a short-term objective, but determining what is missing, as a result of grazing, often is difficult. Herbaceous stubble height is easier to document and communicate than is utilization; that is, it is easier to measure what is still there than to estimate what has been removed and explain it to a varied audience (Leonard et al. 1997, Sanders 1998, Skinner 1998). Residual stubble height serves as an approximate visual guide for a variety of potential grazing impacts and therefore, can be used by the manager to make decisions on livestock use and movement (Hall and Bryant 1995, Skinner 1998).

Overall riparian system response to control of stubble height

Well documented evaluations of riparian area responses to control of streamside

stubble height are limited. One evaluation of a grazing allotment in Montana compared streambank alteration, stubble height, and woody plant and forage utilization as predictors of stream channel cross-section modification. All variables examined had relatively low correlations with stream channel changes, although stubble height and percentage change in stubble height appeared to be the most useful measures (Rhodes et al. 1996).

A study that evaluated use of stubble height criteria was conducted in a central Idaho mountain meadow that had historically experienced heavy cattle grazing during the growing season. Three treatments were applied in the last half of June: no grazing; light grazing (20–25% utilization); and moderate grazing (35–50% utilization) during the 10 year study. Stream width and depth, streambank stability, channel bottom embeddedness, willow cover and height, plant species richness by growth form, plant community-type, and plant and litter cover were among the variables measured. Virtually all streamside variables changed from initial conditions toward conditions more beneficial for salmonid fisheries habitat when pastures were not grazed or when pastures were grazed to a 14 cm streamside stubble height. A lesser number of variables improved when pastures were grazed to a 10 cm streamside graminoid stubble height (Clary 1999). Although this study did not include a stubble height treatment (and associated grazing intensity) that would be too severe for any riparian recovery, we consider that it has provided evidence for defining a critical forage stubble height for the mountain meadow situation studied. Notwithstanding that most measured variables under the 10 cm stubble height treatment responded positively during the 10 year study, several important variables did not recover or recovered very slowly from initial conditions (Clary 1999 and unpublished data). Such a reaction did not occur under the 14 cm stubble height treatment. This suggests that the 10 cm stubble height treatment in this ecosystem approached a degree of grazing stress that could have resulted in a failure of the riparian area to recover.

Research Needs

All is not known about the application of stubble height criteria to the management of riparian grazing. In fact, relatively little direct investigation has been conducted. Additional research is needed to increase the scientific basis for the use of

stubble height as a tool to manage riparian areas. Work is particularly needed in the following areas:

**The determination of where a stubble height guideline is efficient and effective, and where it is not appropriate.* For example, the authors' experience suggest that, for smaller mountain meadow streams that widen under grazing stress, use of stubble height to guide management appears to be very effective. Best Management Practice guidelines developed under the Idaho Agricultural Pollution Abatement Plan (IDEQ-ISCC 1993) suggest that stubble height criteria should be used where streambank stability is dependent upon herbaceous plants. Alternatively, woody plant utilization or streambank disturbance should be used as a management guide in situations where streambank stability is controlled by substrate or the stream is deeply incised.

**Determination of proper stubble heights in high elevation or other sites where species composition and growing conditions result in relatively low statured forage plants.* Even though grazing to a short stubble height in these situations can be acceptable from a plant physiology standpoint, other issues as forage intake, animal movement, and woody plant browsing would still be potential concerns.

**Evaluation of the relative preference of herbaceous vegetation and willows in different seasons under different combinations of herbaceous and woody species, and at different forage stubble heights.* The only quantitative study to date has been in a high elevation, tall sedge community in Colorado.

**Documentation of the direct impacts of livestock on streambanks of different stream types, parent materials, moisture conditions, and livestock occupancy levels as guided by stubble height.*

**Increased understanding of channel evolution and how recovery processes affect the local flood plain watertable and the greenline (Winward 2000) vegetation in relation to different grazing intensities and residual stubble heights.*

Conclusions and Management Implications

The use of stubble height as a grazing management guide is not new and its use has been questioned in some situations. However, as we understand more about the complexities and interactions within riparian areas we realize why this variable has meaningful application there.

Although the direct benefits of maintaining minimum stubble heights may be limited to such items as sustaining forage plant vigor and the stabilization of streambank-building sediments, numerous indirect benefits occur as well. Many of these benefits are related to the physical manner in which cattle graze. When stubble heights are reduced to 7–10 cm, cattle forage intake declines because the tongue sweep becomes ineffective and foraging efforts become less efficient. If stubble heights are maintained at lengths compatible with high forage intake (generally 10 cm or more), substantially less browsing of willows and other riparian shrubs should occur, although about a 20 cm stubble height was required to lessen late summer consumption of willows in a Colorado tall sedge community. The taller the remaining forage heights, the less time cattle have spent grazing on the site. In addition, there is less chance of excessive trailing as livestock search for improved forage supplies to maintain forage intake. Using stubble height to monitor foraging behavior and physical impacts may even be more important than maintaining stubble heights that support plant vigor and sediment deposition (Skinner 1998).

Monitoring of stubble on adjacent drier meadows or uplands (using separate criteria for dry areas) is also important in riparian management. Cattle usually prefer the drier portions of mountain meadows in the spring or early summer because of the avoidance of wetter soils and the preference for the normally more grassy plant composition. As grazing reduces forage stature and the mechanics of cattle foraging change intake rates, the foraging animals will move to areas where taller forage is available; often streamside riparian areas.

One of the most obvious benefits for the use of stubble height as a management guide is the communication factor. As compared to forage utilization (which is a measure of what has been removed), stubble height is easier for people to visualize. This alone makes stubble height a worthwhile measure to use on many riparian grazing areas.

Based on numerous observations by experienced professionals (e.g., A. Winward, E. Cowley, F. Reed, and T. Ratcliff, personal communications) and limited research, we conclude that a streamside stubble height of approximately 10 cm (Fig. 2) may be near optimal in many, but not all, situations when considering a number of riparian issues—such as maintaining forage vigor, entrapping and stabilizing sediment under inundated flow,



a. About right



b. Too short



c. Gone

Fig. 2. The suggested stubble height is similar to the width of one's hand. a. About right, b. Too short, c. Gone.

trampling of streambanks, sustaining forage intake and cattle gains, and diversion of willow browsing—taken as a whole. We recognize that any given height can be satisfactory for some processes and less so for others. Therefore, no single height will likely be optimal for all riparian processes. It appears, however, that the 10 cm height may be the best compromise in many situations.

We anticipate that this criterion will be

most meaningful when applied to sites near the stream edge, that is, areas that can be described as streamside, or near-stream areas of hydrophilic or potentially hydrophilic vegetation. Such areas are the most dynamic and sensitive because of their interaction with moving water, and because moist site woody vegetation is often present. We also anticipate that residual vegetation criteria will be most effective in protecting “small stream” sys-

tems, ones in the approximate range of perhaps a few centimeters to about 5 m in width occurring in meadow settings. Such settings are often associated with C, D, and E stream types (Rosgen 1996). This is roughly equivalent to the Best Management Practice component in Idaho wherein a minimum stubble height is required along the greenline (Winward 2000) at the end of the growing and grazing season if streambank stability is dependent upon herbaceous vegetation. If the streambank stability is controlled by substrate or the channel is incised, other grazing guidelines will be used (IDEQ-ISCC 1993).

The suggestion of a specific streamside stubble height is for the purpose of a *starting point* when initiating improved riparian management, one that can be changed as monitoring indicates. In some situations, 7 cm or even less stubble height may provide for adequate riparian ecosystem function, while under other conditions 15–20 cm of stubble height may be required to reduce willow browsing or to limit animal impact on vulnerable streambanks. Sometimes direct monitoring of browsing or streambank breakdown will be necessary to adequately protect sensitive areas (Bengetyfield and Svoboda 1998). The 10 cm criterion is not suggested for specific application on dry meadows or other similar sites.

Epilogue

No single management approach is best for all situations, nor perhaps is even required for a given situation (Clary and Webster 1989, Ehrhart and Hansen 1997, Larsen et al. 1998). Likewise, no management tool serves all purposes. Stubble height of riparian forages can serve as a direct and indirect (surrogate) guide for gaging *current* grazing impacts. However, this short-term management guide does not fill the role of a long-term management objective. That role is filled by such concepts as Potential Natural Community, Desired Future Condition, or Properly Functioning Condition (Winward 1989, Prichard et al. 1993, Kaufmann et al. 1994). A manager should have a clear picture of the desired ecological structure and function before setting a specific height standard. As ecological succession progresses, the stubble heights that yield the desired results could also change (W. Krueger and Q. Skinner, personal communications).

Short-term management guides are

methods to help the manager attain long-term objectives, but don't represent long-term objectives. Nor do stubble height criteria represent a "management system." The grazing management system selected and applied by the manager should meet both short- and long-term objectives. Remember, a management system or guide is applied to help achieve a goal or objective; the management system or guide is not the objective.

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Erratum

In the September issue of the *Journal of Range Management* the following information was mistakenly left off the author information. The article which began on page 479 through 482 was entitled *Effects of roundups on behavior and reproduction of feral horses* by Kyle V. Hansen and Jeffrey C. Mosley

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Impacts of western juniper on plant community composition and structure

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Abstract

Western juniper (*Juniperus occidentalis* Hook.) has been actively invading shrub steppe communities during the past 120 years. The majority of these stands are still in transition, from early open juniper shrub steppe communities to closed juniper woodlands. In addition, juniper expansion has been occurring across a broad array of soils and topographic positions. Despite the high degree of spatial and developmental heterogeneity, juniper woodlands are frequently treated generically in resource inventories, management, and wildlife habitat assessments. Our goal was to evaluate the impact of western juniper encroachment and dominance on plant community composition and structure across several plant associations. This study was conducted in southeastern Oregon and northeastern California on low sagebrush (*Artemisia arbuscula* Nutt.), mountain big sagebrush (*A. tridentata* spp. *vaseyana* (RYBD.) Beetle), and aspen (*Populus tremuloides* Michx.) alliances. Stages of woodland development across plant associations were categorized into 1 of 4 successional phases (early, mid, late, and closed) based on tree growth and stand structural characteristics. Plant cover by species group, species diversity and richness, bareground cover, soil characteristics, elevation, aspect, and slope were measured in 108, 60 x 46 m macroplots. Twinspan was used to sort plant communities. Regression analysis was used to evaluate the relationship of tree canopy cover to shrub and herbaceous cover. Herbaceous and bareground cover were compared between early and closed stands within plant communities. Woodland structure at stand closure was different among associations varying from 19% cover and 64 trees ha⁻¹ in a low sagebrush community to 90% cover and 1,731 trees ha⁻¹ in an aspen community. Increase in juniper dominance had little impact on low sagebrush and an inconsistent effect on bitterbrush (*Purshia tridentata* Pursh.). In the mountain big sagebrush alliance, sagebrush cover declined to approximately 80% of maximum potential as juniper increased to about 50% of maximum canopy cover. Aspen (*Populus tremuloides* Michx.) also declined as juniper dominance increased. Herbaceous cover and species diversity declined and bare ground increased with increasing juniper dominance in the mountain big sagebrush/Thurber needlegrass association. However, herbaceous cover on the deeper soils characterized by Idaho fescue did not decrease with increasing juniper dominance. To determine

the effect of juniper dominance or woodland management on community composition and structure, plant community and stage of stand development should be identified.

Key Words: *Juniperus occidentalis*, species composition, plant cover

Resumen

Durante los últimos 120 años el “Western Juniper” (*Juniperus occidentalis* Hook.) ha estado invadiendo activamente las comunidades arbustivas de la estepa. La mayoría de estas poblaciones aun están en transición, de comunidades arbustivas de estepa abierta a bosques cerrados de “Juniper”. Además, la expansión del “Juniper” ha estado ocurriendo a lo largo de una amplia variedad de suelos y posiciones topográficas. A pesar del alto grado de heterogeneidad espacial y de desarrollo, los bosques de “Juniper” frecuentemente son tratados genéricamente en los inventarios de recursos y evaluaciones de hábitat y manejo de fauna. Nuestra meta fue evaluar el impacto de la invasión y dominancia del “Western Juniper” en la composición y estructura de la comunidad vegetal a lo largo de varias asociaciones de plantas. Este estudio se condujo en el sudeste de Oregon y en el nordeste de California en asociaciones de “Low sagebrush” (*Asteris arbuscula*), “Mountain sagebrush” (*A. Tridentata* spp. *vaseyana* (Rybd.) Beetle) y “Aspen” (*Populus tremuloides* Michx.). Los estados de desarrollo de los bosques en las asociaciones de plantas se categorizaron en 1 de 4 fases sucesionales (inicial, media, final y cerrada), basadas en el crecimiento de los árboles y las características estructurales de la población. La cobertura vegetal por grupo de especies, la diversidad y riqueza de especies, la cobertura de suelo desnudo, las características del suelo, elevación y pendiente se midieron en 108 macroparcelas de 60 x 46 m. Las comunidades de plantas se ordenaron con Twinspan. El análisis de regresión se utilizó para evaluar las relaciones de la copa de los árboles con la cobertura de arbustos y estrato herbáceo. La cobertura de las hierbas y suelo desnudo se comparó entre poblaciones de bosque cerrados e inicial dentro de las comunidades de plantas. La estructura del bosque en poblaciones cerradas difirió entre las asociaciones variando de 19% de cobertura y 64 árboles ha⁻¹ en la comunidad de “Low sagebrush” a 90% de cobertura y 1,731 árboles ha⁻¹ en una comunidad de “Aspen”. El aumento en la dominancia del “Juniper” tuvo impacto en la comunidad de “Low sagebrush” y un efecto inconsistente en la comunidad de “Bitterbrush” (*Purshia tridentata* Pursh.). En la asociación de “Mountain big sagebrush” la cobertura de “Sagebrush” disminuyó a aproximadamente 80% del máximo potencial conforme el la cobertura de copa del “Juniper” incremento a aproximadamente 50%. El “Aspen” (*populus tremu-*

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loides Michx.) También se redujo conforme la dominancia del "Juniper" incrementó. En la asociación "Mountain big sagebrush"/"Thuber needlegrass la cobertura de herbeceas y la diversidad de especies disminuyó y la cobertura de suelo desnudo aumento al aumentar la dominancia del "Juniper". Sin embargo, la cobertura herb-acea en suelos profundos, caracterizados por "Idaho fescue", no se redujo con el aumento de la dominancia del "Juniper" Para determinar los efectos de la dominancia del "Juniper", o del manejo del bosque, se debe identificar la composición y estructura de la comunidad vegetal y el estado de desarrollo de la población.

Conversion of shrub steppe communities in the Intermountain West to *Juniperus* woodlands has been an active process during the past 120 years (Tausch et al. 1981, West 1984, Miller and Wigand 1994, West et al. 1998). Over 90% of the 3.2 million ha of western juniper (*Juniperus occidentalis* Hook.) woodlands have developed in the last 100 years (USDI-BLM 1990). Prior to European settlement juniper was primarily confined to rocky ridges or surfaces with sparse vegetation (Cottam and Stewart 1940, Barney and Frishknecht 1974, West 1984). However, newly formed juniper woodlands now occupy more productive sites with deep well drained soils (Burkhardt and Tisdale 1969, Tausch et al. 1981, West 1984, Miller and Rose 1995). The replacement of shrub steppe communities with juniper woodland during the past 130 years has been largely attributed to reduced fire frequency (Burkhardt and Tisdale 1976, Miller and Rose 1999). Heavy livestock grazing between 1880 and 1930 removed fine fuels (herbaceous biomass), which previously had carried the fires. In addition, fire suppression, especially following WWII, further reduced the role of fire. Aboriginal Americans may also have impacted juniper and pinyon woodlands over thousands of years through their influence on fire regimes and possibly were partially responsible for the loss of large browsers at the end of the Pleistocene (West 1999).

Western juniper woodlands dominate large areas of land and occupy a broad array of environments. However, despite the heterogeneity of the landscape occupied by juniper and the various stages of stand development occupying these landscapes, juniper woodlands are frequently treated generically in management, resource inventories, and wildlife habitat

assessments. There is limited research evaluating the relationship between increasing juniper dominance and associated understory response across different range sites. Most studies on western juniper have addressed fairly specific questions on individual sites (e.g., Adams 1975, Young et al. 1985, Vaitkus and Eddleman 1991, Bates et al. 1998, 2000). It is difficult to compare and contrast existing western juniper research because there is no contextual basis for evaluating stands. Given the diverse landscapes occupied by western juniper, it is very likely that stand development and understory/overstory relations will be strongly influenced by soils, aspect, elevation, etc. In addition, the wide variety of woodland developmental stages occupying these landscapes will also affect composition and structure of the understory. The response of understory vegetation to juniper removal may be entirely different at early versus late stages of stand development. The development of juniper woodlands in sagebrush and aspen communities also alters habitat for wildlife.

There are many classification guides that describe sagebrush steppe and western juniper communities (Driscoll 1964, Franklin and Dyrness 1988, Anderson et al. 1998), yet none provide any detail on western juniper succession. Most of the classification guides attempt to group existing communities, many of which are in early to middle stages of woodland development, rather than describing community dynamics. While classification guides are useful tools for land managers, not recognizing transitional states of juniper encroachment combined with the generic treatment of western juniper woodlands has caused confusion in wildlife habitat evaluations (Maser and Gashwiler 1978, Puchy and Marshall 1993), environmental debates (Belsky 1996), assessments of erosion potential (Buckhouse and Mattison 1980), and general discussions of juniper ecology. Knowledge of community differences, successional patterns, and trajectories are essential for long-term management planning.

This study was designed to provide a context for comparing communities and successional stages associated with western juniper. The objective of the study was to evaluate the influence of juniper dominance on plant community composition and structure across several major plant associations (Grossman et al. 1998) commonly linked with western juniper¹. Our specific hypotheses were: 1) the impacts of juniper on understory structure and composition varies among associations; 2) at full woodland development, tree densi-

ty, and cover are different among associations; and 3) within a plant association there are predictable thresholds of juniper dominance, beyond which disturbance pattern and understory species are negatively impacted.

Materials and Methods

Study Area

The study areas were located in the High Desert and Klamath Ecological Provinces in southeastern Oregon and northeastern California (Fig. 1) (latitudes to 43°70' to 41°00', longitudes 120°45' to 118°00') where western juniper typically dominates communities between 1,370 and 2,100 m in elevation. Parent materials across these 2 provinces are predominately of igneous origin. A combination of basin and range, and weathered mountains of volcanic origin characterize the topography. Climate is cool and semi-arid, characteristic of the northern Intermountain region. Precipitation in the juniper zone across the 2 provinces typically varies between 300 to 400 mm (Taylor 1993). It is received primarily as snow in November, December, and January, and as rain in March through June.

Plant communities occurring among the 5 study locations (Fig. 1) are characteristic of high desert communities commonly associated with western juniper. Three alliances selected for study were, low sagebrush (*Artemisia arbuscula* Nutt.), mountain big sagebrush (*A. tridentata* spp. *vaseyana* (RYBD.) Beetle), and aspen (*Populus tremuloides* Michx.)². Aspen stands were associated with shrub steppe communities in the Steens Mountain and south Warner Mountains study areas below 2,100 m. Study sites spanned from aspen on deep loamy soils to low sagebrush on shallow heavy clay soils, thus providing a variety of communities, soils, landforms, and topographic positions. Elevation of study plots ranged between 1,450 to 2,100 m.

Plot Selection

To evaluate the effects of juniper succession we substituted space for time by

¹Nomenclature follows physiognomic-floristic hierarchy from Grossman et al. 1998; an alliance is defined by the dominant/diagnostic species of the upper most stratum followed by an association, defined by an additional dominant/diagnostic species from any strata.

²Nomenclature follows Hitchcock and Cronquist 1973, and Cronquist et al. 1977.

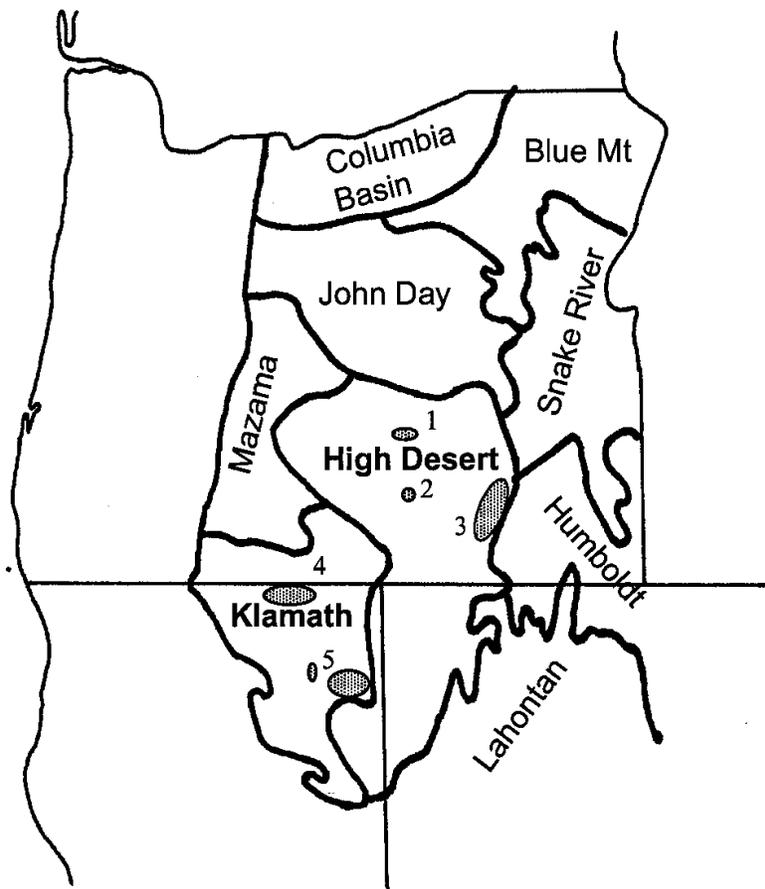


Fig. 1. Five study sites; 1 = Northern Great Basin Experimental Range, 2 = Juniper Mountain, 3 = Steens Mountain, 4 = Devils Garden, and 5 = south Warner Mountains located within the High Desert and Klamath Ecological Provinces (Derived from Anderson et al. 1998, and Bailey 1994). Surrounding provinces are also shown.

evaluating plant communities in different stages of woodland development. We selected stands that represented a large proportion of the 2 ecological provinces and elevations in which western juniper is actively expanding. Stands were grouped into soil and plant associations that dominate much of this landscape, with the primary variable being the relative abundance of western juniper. To reduce variability we attempted to select communities that appeared not to have been significantly altered by heavy grazing or recent fires. Specific criteria used for plot selection were: (1) soils that were common to the area based on existing soil classification maps; (2) communities dominated by low sagebrush, mountain big sagebrush, or aspen with a herbaceous understory dominated by Sandberg bluegrass (*Poa sandbergii* Vasey) in the low sagebrush alliance; Thurber needlegrass (*Stipa thurberiana* Piper), bluebunch wheatgrass (*Agropyron spicatum* Scribn. & Smith), Idaho fescue (*Festuca idahoensis* Elmer),

Columbia needlegrass (*S. columbiana* Macoun), or western needlegrass (*S. occidentalis* Thurber) in the mountain big sagebrush alliance; and California brome (*Bromus carinatus* Hook. & Arn.) or Letterman's needlegrass (*S. lettermanii* Vasey) in the aspen alliance; (3) stands that represented different stages of woodland development; (4) sites where disturbance (grazing, weed invasion, roads, etc.) had not significantly altered the community; and (5) sites that had not burned within the last 50 years. The initial classification of plant communities in the field was based on the relative abundance of the species listed above. In closed woodlands, remnant shrubs were used as indicators for community classification. In several aspen macroplots where juniper completely dominated the overstory, the presence of large down dead aspen were used to classify the site. In addition, juniper dominated aspen stands were selected on the basis of having similar soils and topographic position as aspen dominated stands.

Woodland development phases were categorized into 1 of 4 successional phases: early, mid, late, and closed, based on annual tree growth and stand structural characteristics (Miller et al. 1999a). Tree growth characteristics used were annual lateral and terminal leader growth on sapling and full size trees. Stand structure characteristics used were tree cover, height, and proportion of live and dead shrub canopy. The early phase of stand development contained < 5% juniper cover and sapling juniper (< 3m tall) with vigorous lateral and terminal leader growth. Leader growth often exceeded 10 cm per year. Early development juniper stands also contained a nearly intact shrub layer. The key characteristic for stand closure is limited sapling leader growth, typically < 2 cm per year. However, terminal leader growth still may exceed 6 cm per year on canopy dominant trees in late successional and closed stands. We attempted to locate macroplots within each association in the 4 different phases of woodland development. Table 1, derived from Miller et al. (1999a), was modified using data collected in this study.

Plot Measurements

Plant composition and soil characteristics were measured in 108, 60 x 46 m macroplots across the 5 study areas (derived from Poulton and Tisdale 1961). Three parallel 60 m transects located 14 m apart within each macroplot were used to measure juniper and aspen canopy cover with the line intercept method. Density and height of juniper and aspen > 30 cm tall were measured in three, 6 x 60 m belt transects centered on the 60 m cover transects. Density of juniper trees < 30 cm were recorded in a 2 x 30 m belt transect also centered on the cover transects. Three, 30 m lines, located on the 60 m transect were used to measure shrub cover by species with the line intercept technique. Cover of herbaceous species, litter, bare ground, and rock were estimated in 0.20 m² plots placed at 3 m increments along each of the three, 60 m transects (n = 60/macroplot). We recorded whether a plot was located beneath the tree canopy or in the interspace.

A soil pit was dug near the center of each macroplot. Soils were described and samples collected within each horizon for textural analysis. Soil texture was measured in the laboratory with the hydrometer method of particle size analysis (Gee and Bauder 1986). Aspect, slope, and elevation were also measured. Rill and gullies were noted if present on a site to provide indirect evidence of soil movement.

Table 1. Characteristics of transitional stages during western juniper woodland succession in several mountain big sagebrush associations. Estimated maximum juniper cover is 25–41% in Thurber needlegrass, 34–58% in Idaho fescue, and 60–75% in Columbia needlegrass associations.

Characteristics (Post Settlement Stands)	Early	Mid	Late	Closed
Tree Canopy (% of Max Potential)	Open, actively expanding 10%	Actively expanding 10 to 49%	Expansion reduced 50 to 80%	Expansion nearly stabilized > 80%
Leader Growth (Dominant Trees) (cm/yr)	Leader growth terminal >10 lateral >10	Leader growth terminal >10 lateral >10	Leader growth terminal >10 lateral <10	Leader growth terminal >10 lateral <6
Crown Lift ² (Dominant Trees)	Absent	Absent	Lower limbs beginning to die where tree canopy > 40%	Present where tree canopy > 40%
Potential Berry production	Low	Moderate to high	Low to moderate	Low to near absent
Tree Recruitment	Active	Active	Reduced, limited primarily to beneath trees	Absent
Leader Growth (Understory Trees)	Leader growth (cm/yr) terminal >10 lateral >6	Leader growth (cm/yr) terminal >10 lateral >6	Leader growth (cm/yr) terminal <10 lateral <6	Leader growth (cm/yr) terminal <6 lateral <2
Shrub Layer	Intact	Nearly intact to significant	75% dead thinning	90% dead

¹During the late and closed stages of succession, leader growth in mature trees is usually confined to the upper 1/3 of the canopy.

²Crown lift is the mortality of lower tree limbs usually due to shading from neighboring trees.

Analyses

Twinspan, a two-way indicator of species analysis, was used to verify and resort initial classification of communities made in the field (Gauch 1982). The grouping of communities into associations was based on relative plant species abundance using cover data. Assimilation tables were developed to describe plant assemblages and physical characteristics for each community. Regression analyses was used to evaluate the relationship of tree canopy cover to shrub and herbaceous canopy cover. A student-t test was used to compare herbaceous and bareground cover in the tree interspace between early and closed juniper stands within an associa-

tion. We conducted analyses on associations with at least 3 macroplots in each of the early and closed transitional stages. Hill's diversity indices, species number (N0), Shannon's index (N1), and Simpson's index (N2), were calculated for early and closed stands using cover data. Neither mountain big sagebrush nor western juniper were included in diversity and richness indices. Mean diversity indices for macroplots in open and closed stands within associations are reported. ANOVA and Duncan's New Multiple Range Test were used to compare juniper canopy cover and density at stand closure between associations (SAS 1996).

Results

Associations

Twinspan separated out several major associations (Table 2). Low sagebrush/Sandberg bluegrass: This association was typically found on clayey montmorillinitic frigid Lithic Argixerolls ranging between 20 and 60 cm deep underlain by fractured basalt. Several sites were also classified as Lithic Durargids. Slopes were < 2%. Herbaceous species characterizing this association were Sandberg bluegrass, onespoke oatgrass (*Danthonia unispicata* (Thurb.) Munro ex Macoun), Idaho fescue (beneath the juniper canopies), nineleaf

Table 2. Plant associations sampled where n>3. Groupings were done by Twinspan (total n = 108).

Association	Sample size	Elevation Range (mean)	General Aspect	Slope	Soils A & B Horizons
Low sagebrush/Sandberg bluegrass	12	(m) 1482–1824 (1626)	None	(%) <2	A: Shallow clay loam to clay B: clay
Mountain big sagebrush/ Thurber needlegrass	15	1575–1990 (1737)	Southerly	8–22	A: Sandy clay loam to clay loam B: Sandy clay loam to silty clay loam
Bluebunch wheatgrass	5	1545–1890 (1715)	South to West	8–26	A: Sandy to clay loam B: Clay loam to clay
Idaho fescue	49	1525–2006 (1723)	Northwest to Southeast	0–45	A: Loam to clay loam B: Clay loam to clay
–Mountain snowberry/ Columbia needlegrass	12	1560–2100 (1846)	Northwest to Northeast	10–25	A&B: Loam
Quaking aspen	15	1780–2045 (1906)	North to East	8–35	A&B: Loam

lomatium (*Lomatium triternatum* (Pursh) Coult. & Rose), scabland penstemon (*Penstemon duustus* Dougl. Ex Lindl.), white paintbrush (*Castilleja pilosa* (Wats.) Rydb.), and ballhead sandwort (*Arenaria conjestus* Nutt.).

Mountain big sagebrush/Thurber needlegrass: This was the driest of the mountain big sagebrush communities sampled, typically occurring on southerly aspects. This association was commonly found on loamy, sandy loam, and fine-loamy, skeletal mixed frigid Argixerolls. Soil varied between 36 and 67 cm in depth across the macroplots, and were frequently underlain by a duripan. Bluebunch wheatgrass ranged from a trace to co-dominating with Thurber needlegrass. Common forbs were tailcup lupine (*Lupinus caudatus* Kell.), basalt milkvetch (*Astragalus filipes* Torr.), Hoods phlox (*Phlox hoodii* Rich.), western hawkbeard (*Crepis occidentalis* Nutt.), sagebrush mariposa (*Calochortus macrocarpa* Dougl.), and nineleaf lomatium.

Mountain big sagebrush/Bluebunch wheatgrass: This association occurred on south to west facing slopes on well drained to moderately drained soils. Soil depths varied between 45 and 80 cm. Common forbs were similar to those found in the Thurber needlegrass communities.

Mountain big sagebrush/Idaho fescue: Soils commonly found in this association were loamy to clayey, skeletal, mixed to montmorillintic Typic to Pachic Argixerolls. Soil depths ranged between 65 and 100+ cm. On Steens Mountain the majority of these communities were located on northerly aspects, particularly below 1,800 m. However, a few plots were located on southerly aspects. On the Devils Garden, slopes were typically less than 10% with mixed aspects. Herbaceous species common in this association were prairie junegrass (*Koeleria cristata* Pers.), twin arnica (*Arnica sororia* Greene), nodding microseris (*Microseris nutans* (Geyer) Schultz-Bip.), common yarrow (*Achillea millefolium* L.), parsnip-flowered eriogonum (*Eriogonum heracleoides* Nutt.), one-stemmed butterweed (*Senecio integerrimus* Nutt.), and speckle-pod milkvetch (*Astragalus lentiginosus* Dougl.). Twinspan further divided this association into 3 subgroups. The first division separated south Warners from the Devils Garden and the Oregon study sites (see Figure 1 for locations). The second division separated the Devils Garden study area from the Oregon study sites. Soils were similar across the 3 subgroups. However several unique species distin-

guished the 3 subgroups. Species distinguishing south Warners were woolly mule's ear (*Wyethia mollis* Gray), barestem buckwheat (*Eriogonum nudum* Dougl.), wavy-leaved paintbrush (*Castilleja applegatei* Fern.), desert gooseberry (*Ribes velutinum* Greene), and spurred lupine (*Lupinus laxiflorus* Dougl.). The relatively low abundance of forbs in the Devils Garden macroplots compared to the Oregon study sites was the primary difference separating these 2 subgroups.

Mountain big sagebrush—mountain snowberry (*Symphoricarpos oreophis* Gray)/Columbia needlegrass (western needlegrass): This association, typically located on northerly aspects with deep loamy soils, was the most productive of the mountain big sagebrush associations sampled. This association also had the greatest diversity of shrubs compared to other communities. Soils were generally loamy mixed frigid Pachic Haploxerolls, > 80 cm deep. The dominant understory grass characterizing this association on Steens Mountain, Columbia needlegrass, shifted to western needlegrass in the south Warner study area. Common herbaceous species in this association were California brome, Ross' sedge (*Carex rossii* Boot), short-beaked agoseris (*Agoseris glauca* (Pursh) Raf.), one-stemmed butterweed, nodding microseris, long-flowered bluebells (*Mertensia longiloba* Greene), and ballhead waterleaf (*Hydrophyllum capitatum* Dougl.).

Quaking aspen: These stands were situated on north to northeast aspects and were the most mesic of the rangeland cover types measured. Soils were typically loamy to fine-loamy mixed frigid Pachic

Haploxerolls to Haplocryolls, > 100 cm in depth. Common understory species were California brome, Letterman's needlegrass, bearded wheatgrass (*Agropyron caninum* (L.) Beauv.), Menzie's silene (*Silene mezesii* Hook.), nodding microseris, ballhead waterleaf, veiny meadowrue (*Thalictrum venulosum* Trel), and starry solomon (*Smilacina stellata* (L.) Desf.).

Closed woodland structure

Both cover and density of juniper trees (> 3m) at stand closure were significantly different (p < 0.0001) across associations (Table 3). Woodland canopy cover of closed stands ranged as low as 19% in a low sagebrush/Sandberg bluegrass community to a high of 90% in an aspen community. Tree density also varied widely across communities ranging between 64 and 1,731 trees ha⁻¹ in closed stands. As woodland development approached stand closure, maximum density of young trees (< 3m in height) declined (Fig. 2).

Shrub and aspen canopy

The relationship between low sagebrush and juniper canopy cover was not significant (p > 0.05). The only area where low sagebrush was noticeably absent was directly beneath the juniper canopy. However, there was a strong relationship between juniper and mountain big sagebrush canopy cover (Fig. 3). As juniper canopy cover increased mountain big sagebrush canopy declined. When juniper canopies reached 50% of maximum woodland cover, the shrub layer declined to 80% of maximum potential in the moun-

Table 3. Mean and range of juniper cover and density (trees > 3m tall) in closed stands for 6 associations. Means followed by different letters were significantly different (p < 0.0001) for cover or density between associations.

Association	% Cover (range)	Trees Ha ⁻¹ (range)
	(%)	
Low sagebrush/Sandberg bluegrass (n=4)	21 ^a (19–24)	84 ^a (64–111)
Mountain big sagebrush/Thurber needlegrass (n=6)	34 ^b (25–41)	346 ^b (222–481)
Mountain big sagebrush/bluebunch wheatgrass (n=2) ¹	43 (35–47)	345 (260–444)
Mountain big sagebrush/Idaho fescue (n=15)	48 ^c (34–58)	479 ^c (247–716)
Mountain big sagebrush–snowberry/Columbia needlegrass (n=1) ¹	63	889
Quaking aspen (n=3)	84 ^d (78–90)	1319 ^d (906–1731)

¹Not included in analysis because n < 3.

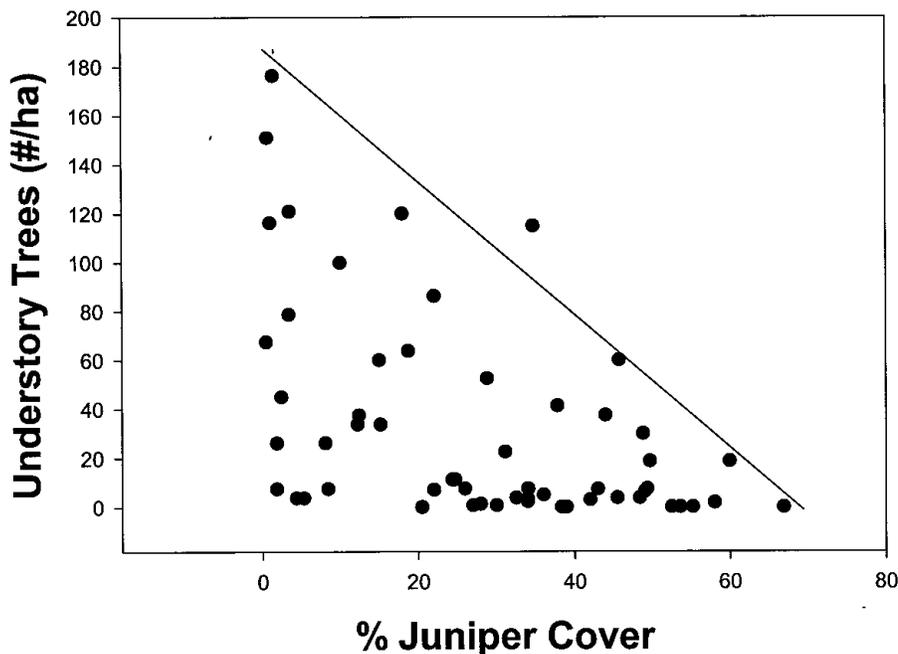


Fig. 2. The relationship between understory juniper tree density (trees <3m tall) and mature overstory tree canopy cover for the mountain big sagebrush/Idaho fescue association. The line represents a boundary layer of maximum juvenile juniper trees occurring with varying juniper overstory canopy cover.

tain big sagebrush/Thurber, mountain big sagebrush/Idaho fescue, and mountain big sagebrush-snowberry/Columbia needlegrass associations. Limited cover values and high variability for other shrub species made it difficult to evaluate their relationship with juniper cover. However, for the more frequently occurring species, increasing juniper cover appeared to have little effect on mountain snowberry and wax current (*Ribes cereum* Dougl.) in mountain big sagebrush—snowberry-Idaho fescue or aspen communities. We did not observe an increase in dead skeletons for these 2 species as juniper canopy increased. The response of bitterbrush (*Purshia tridentata* Pursh) to increasing juniper dominance was inconsistent. Several closed juniper stands contained 80% dead bitterbrush, while 3 closed stands showed little bitterbrush mortality and active recruitment. We measured only 2 curleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) stands that contained a closed juniper canopy. In both stands > 90% of the curleaf mountain-mahogany canopy was dead.

There was a very strong inverse relationship between juniper and aspen overstory canopy cover ($p < 0.0001$) and density ($p < 0.003$) (Fig. 4). As juniper overstory canopy increased, aspen saplings did not replace dying aspen overstory trees.

Herbaceous understory and bare-ground

Response of herbaceous understory cover to juniper was different among associations. In the low sagebrush/Sandberg bluegrass association herbaceous cover

was not different between early stands and stands with maximum juniper cover (Table 4). However, closed juniper stands in the low sagebrush/Sandberg bluegrass association did not fit the criteria developed in Table 1. It was difficult to determine if this association was near maximum juniper cover at 21%. Perennial grass dominance shifted from Sandberg bluegrass in the interspace to Idaho fescue beneath the juniper canopy where grass cover typically exceeded 65%.

Herbaceous cover in the tree interspace in the mountain big sagebrush/Thurber needlegrass association was 69% less ($p < .001$) in closed juniper woodlands compared to early stands (Table 4). The perennial grass component was significantly less in closed versus early stands. Perennial forbs as a group accounted for 2% of the ground cover, were highly variable, and were not significantly different between open and closed stands. There was a significant relationship ($r^2 = 0.865$, $p = 0.0001$) between juniper and total perennial herbaceous cover in this association (Fig. 5). When juniper cover reached 50% of the predicted maximum, perennial herb cover declined to 5.7%.

Herbaceous cover in the tree interspace was not different between early and closed mountain big sagebrush/Idaho fescue juniper stands at Steens, Juniper Mountain, and Devils Garden study areas (Table 4).

Table 4. Perennial herbaceous cover (%) and sample size for early and closed stages of woodland development across associations.

Association	Early (% cover)	n	Closed (% cover)	n	p
Low sagebrush/Sandberg bluegrass		5		4	
P. Grass	8		11.1		ns
P. Forb	4.1		4.4		ns
Total	12.1		16.5		ns
Mountain big sagebrush/Thurber needlegrass		5		7	
P. Grass	14		4		.001
P. Forb	2		1		ns
Total	16		5		.001
Mountain big sagebrush/Idaho fescue Devils Garden		6		9	
P. Grass	7.8		9.9		ns
P. Forb	2.1		1.1		ns
Total	9.9		11		ns
Mountain big sagebrush/Idaho fescue Steens		9		6	
P. Grass	16		15		ns
P. Forb	16.5		12		ns
Total	32.5		27		ns
Quaking aspen		8		3	
P. Grass	9.5		4.4		ns
P. Forb	5		7.3		ns
Total	14.5		11.7		ns

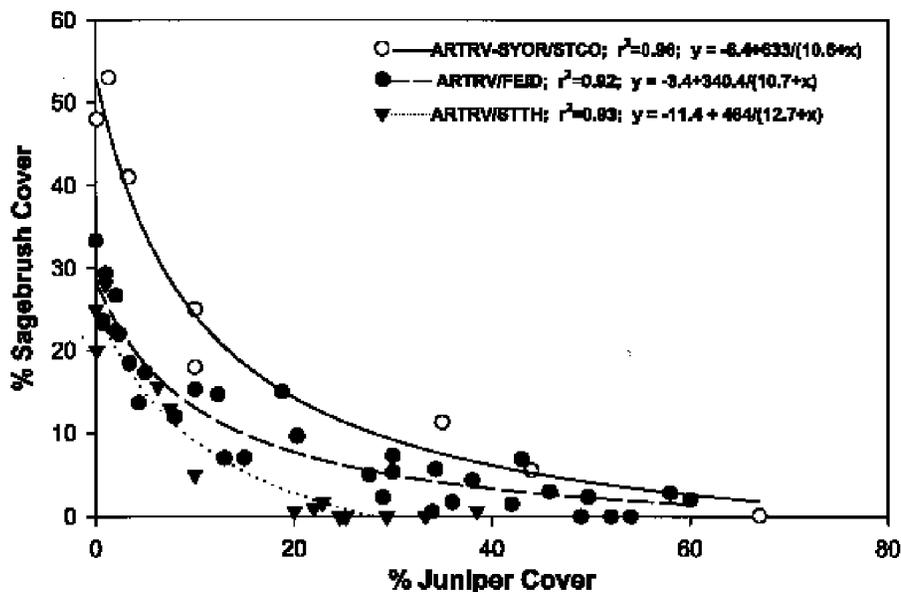


Fig. 3. The relationship between juniper and mountain big sagebrush cover for the mountain big sagebrush/Thurber needlegrass (ARTRV/STTH), mountain big sagebrush/ Idaho fescue (ARTRV/FEID), and mountain big sagebrush-snowberry/Columbia needlegrass (ARTRV-SYOR/STCO) associations.

Nor was there a difference between perennial grass or forb cover between closed and early woodlands. We were unable to locate closed stands within this association in the South Warner study area where woodlands ranged from early to mid development within this association. Regression analysis also showed no significant relationship between juniper cover and herbaceous cover across the different stages of woodland development in the mountain big sagebrush/Idaho fescue and mountain big sagebrush-snowberry/Columbia needlegrass communities.

There was no significant difference in herbaceous cover in aspen stands where juniper was in the early stages of encroachment compared to stands where juniper dominated the overstory. The lack of significance was probably due to the high degree of variability in herb cover across aspen stands regardless of juniper abundance. However, in one aspen macroplot containing nearly 1,000 juniper trees ha⁻¹ and heavy needle deposition due to crown lift (leaf canopy lifts from the ground due to lower limb mortality), perennial herb cover accounted for only 2%. The most abundant herbs in this stand were 4 annuals, pink microsteris (*Migrostis gracilis* Hook.), small-flowered blue-eyed Mary (*Collinsia parviflora* Lindl.), smallflowered woodlandstar (*Lithophragma parviflora* (Hook.) Nutt.), and miner's lettuce (*Montia perfoliata* (Donn) Howell).

Percent bare ground was consistent with herbaceous cover results (Table 5). Percent bare ground was not greater in the tree interspace between closed stands and early stands of woodland development across the low sagebrush/Sandberg bluegrass, mountain big sagebrush/Idaho fescue, and aspen associations. However, in the mountain big sagebrush/Thurber needlegrass association bareground in the tree interspace was significantly greater in the closed stands compared to early woodlands.

Diversity

Species diversity indices were consistently lower in closed juniper woodlands in the mountain big sagebrush/Thurber needlegrass association compared to woodlands in the early development stage

(Table 6). Indices appeared similar between early and closed stands in the low sagebrush/Sandberg bluegrass, and aspen communities, and mountain big sagebrush/Idaho fescue Oregon subgroup. However, the mountain big sagebrush/Idaho fescue for the Devils Garden subgroup was not consistent with the Oregon sites. Species diversity indices, N1 and N2, were lower in the closed stages of woodland development compared to the early phase. This may be due to an increase in perennial grass dominance and a decline in forb abundance under closed stands.

Discussion

The need for sound information on western juniper succession arises from the fact that the majority of western juniper woodlands have not yet reached full development. In addition, this species is still rapidly expanding its range. Gedney et al. (1999) reported that 65% of the 0.9 million ha of western juniper woodland in Oregon had less than 30% tree canopy cover. An additional 1.1 million ha of western juniper were classified as savanna (< 10% tree cover). If juniper woodland canopy cover can potentially exceed 30% in many mountain big sagebrush associations and 20% in low sagebrush associations at stand closure this would indicate that the majority of the 2 million ha of western juniper in Oregon are still in transition from shrub steppe to juniper woodland.

Stand Development

The lack of a well-defined system for identifying stage of stand development has contributed to controversies over western juniper ecology and management. For example, during early stages of stand development with low tree cover (< 5%), mountain big sagebrush cover is still an

Table 5. Percent bareground in the tree interspace for 5 associations.

Association	Open		Cover		Prob
	(%)	n	Closed (%)	n	
Low sagebrush/Sandberg bluegrass	56	5	54	4	ns
Mountain big sagebrush/Thurber needlegrass	55	5	90	7	.001
Mountain big sagebrush/Idaho fescue (Devils Garden)	34	6	32.4	9	ns
Mountain big sagebrush/Idaho fescue (Steens)	16	9	18	6	ns
Quaking aspen	5	8	3.8	3	ns

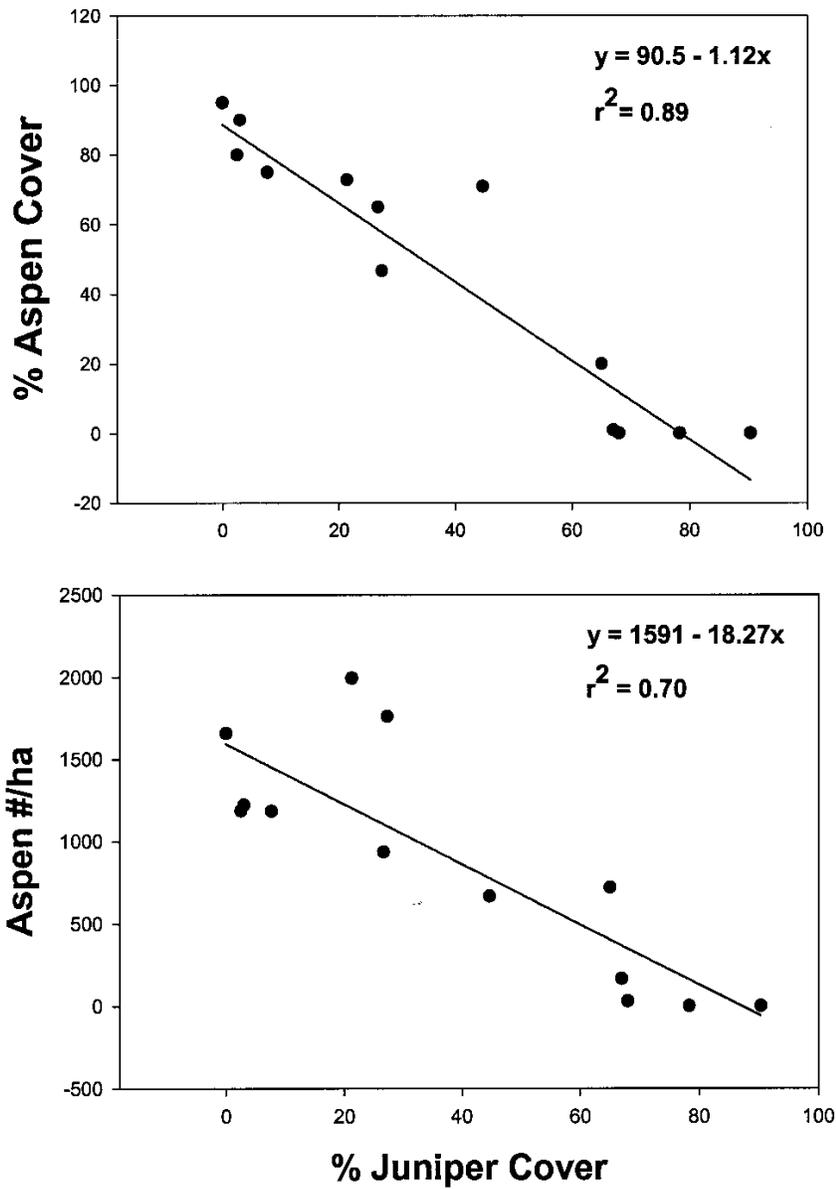


Fig. 4. The relationship between juniper canopy cover and aspen canopy cover ($p < 0.0001$) and density ($p < 0.003$).

important component in the understory providing structural diversity (Fig. 3). However, as juniper cover increases to half of its maximum potential for the site, mountain big sagebrush cover is reduced by 80%. Thus, in a discussion of juniper impacts on sagebrush cover, it is critical to define both the stage of stand development and plant community involved. There appear to be repeatable stand characteristics in the mountain big sagebrush alliance that can be used to define the stage of stand development, regardless of association and site potential (Table 1). Many of the characteristics used in Table 1 relate to the degree of site domination by western juniper. As juniper increases in domi-

nance, woody species such as mountain big sagebrush, bitterbrush, mountain mahogany, and aspen decline (Figs. 3 and 4), and intraspecific competition reduces leader growth and berry production of juniper. There is also a reduction in juniper recruitment as stand development progresses (Fig. 2).

During woodland succession the decline in mountain big sagebrush canopy is not proportional to the increase in juniper canopy. As juniper approaches 50% of maximum potential canopy cover in mountain big sagebrush communities, mountain big sagebrush declines to about one fifth of maximum canopy cover (Fig. 3). In southwest Utah pinyon-juniper com-

munities, Tausch and West (1995) reported shrubs declined to one fourth of maximum when pinyon-juniper cover reached 50% of maximum. Throughout the Intermountain West, big sagebrush has been reported to decline with the increase in juniper or pinyon (Cottam and Stewart 1940, Adams 1975, West 1984, Tress and Klopatek 1987, Tausch and West 1995). Although we measured a decline in bitterbrush canopy and an increase in shrub skeletons with the increase of juniper, the response of bitterbrush was not consistent. In central Oregon, Adams (1975) reported a decline in big sagebrush, bitterbrush, and rabbitbrush (*Chrysothamnus viscidiflours*) with an increase in western juniper canopy. However, Adams concluded that existing plants of bitterbrush lived out their normal life span during woodland development but recruitment was drastically limited. We observed both scenarios of limited and active bitterbrush recruitment under closed stands. Juniper also readily invaded aspen stands. Both aspen density and cover declined as juniper canopy cover increased. In the absence of fire, juniper will likely continue to invade and replace aspen stands within the juniper woodland belt, below 2,130 m (Miller and Rose 1995, Wall 1999).

In our study, the response of herbaceous species to increasing juniper dominance was not consistent. In the literature, the report of declining native herbaceous vegetation as juniper and or pinyon increases is generally consistent (Arnold 1964, Blackburn and Tueller 1970, Meeuwig and Cooper 1981, Tausch et al. 1981, Everett and Sharrow 1985, Tausch and West 1995). However, the majority of these studies were conducted on heavily disturbed sites. One exception, a study conducted on a site with a past history of over-grazing, found an increase in herbaceous production with increased tree size (Vitakus and Eddleman 1991). However, in northwestern California, Evans and Young (1985) found that evaluating the effect of western juniper on the herbaceous understory was difficult because of past heavy grazing and the dominance of introduced annuals. In our study, stands were lightly to moderately disturbed and weed invasion was minimal. In this region the threat of weed invasion is generally thought to be greatly reduced above 1500 m. The response of herbaceous plant cover in the mountain big sagebrush/Thurber needlegrass association fit the hypothesis that understory vegetation declines as tree dominance increases. The majority of these soils have a restrictive layer between

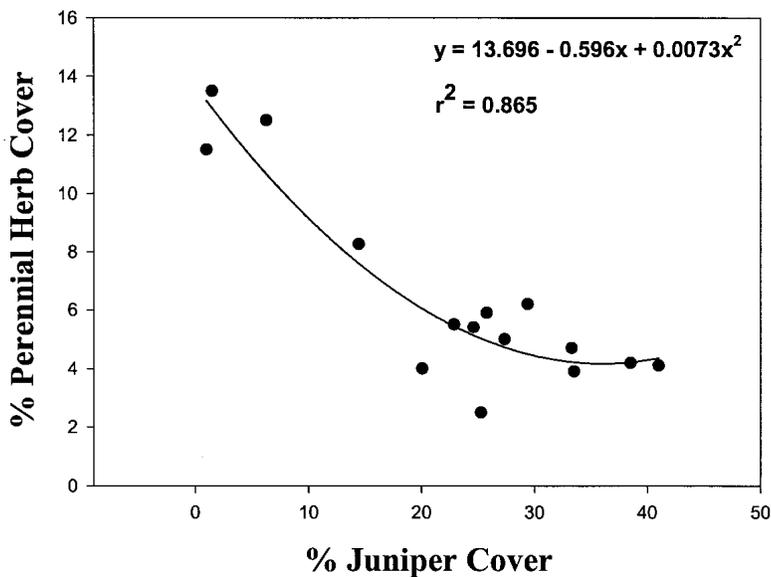


Fig. 5. The relationship between perennial herb and juniper cover in the mountain big sagebrush/Thurber needlegrass association.

30 and 50 cm deep. We observed a very high density of juniper roots in the soil layer above the duripan in our soil pits. Few roots were observed to penetrate the duripan. In this same association, Bates et al. (2000) reported a 3 fold increase in herbaceous cover during the second growing season following western juniper removal. The soils on this study site were 40 to 50 cm deep underlain by a thick duripan, which limited root penetration. However, in the mountain big sagebrush/Idaho fescue association, herbaceous cover between early and closed woodlands was similar. These sites occupied deeper soils underlain by fractured bedrock. In the soil pits, we observed a lower concentration of juniper roots in the upper 50 cm. The lack of herbaceous response to increasing juniper may also be partially attributed to Idaho fescue being well adapted to growing beneath conifer canopies. Unfortunately we were unable to locate enough late to closed woodlands in the Columbia needlegrass association to determine if deep well drained soils and/or species adaptability is the key to the persistence of the herb layer. Herbaceous composition and cover in aspen stands was highly variable. However, in a stand dominated by juniper where heavy conifer needle deposition occurred due to crown lift, herbaceous cover was 2% and primarily composed of annuals. Wall (1999) reported a significant decrease in herbaceous cover as juniper dominance increased in aspen stands.

The amount of bareground in the tree interspace was greater in closed stands compared to earlier stages of development

only in the mountain big sagebrush/Thurber needlegrass association. Although juniper cover averaged 34% in closed stands, little plant or litter cover protected the interspace, which accounted for 66% of the total area. We observed considerably more surface soil movement in this association than in any other association. Greater potential sediment loss has been reported for western juniper communities compared to adjacent shrub steppe communities (Buckhouse and Mattison 1980). Davenport et al. (1998), however, concluded that pinyon-juniper contributed to accelerated erosion only on certain soil types. An increase in pinyon and juniper had little

effect on sediment loss on soils with low erosion potentials but did increase soil loss where soils were highly erosive. They found plant cover in the tree interspace played an important role in reducing sediment loss on highly erosive soils.

Climax

Although a frequently debated ecological term, climax has often been applied to juniper and pinyon pine woodlands. McCune and Allen (1985) defined climax as "a relatively stable composition that develops in the absence of major disturbance". Since many woodlands exhibit very low dynamism, West and Van Pelt (1987) felt climax is a good working definition of a possible result of succession towards closed woodlands. Since the life span of western juniper can exceed 1,000 years (Miller et al. 1999b) it would appear that once a woodland has closed, the site will remain a woodland, in the absence of a major disturbance. However, major disturbance events that have shifted relatively stable closed woodlands to other steady states or seral stages are severe droughts in the Southwest (Bentancourt et al. 1993) and extreme fire conditions creating crown fires in dense pinyon-juniper woodlands (West 1999).

At climax, woodland structure and composition varied with site potential across the landscape. The 6 associations we sampled represent a major portion of the landscape heterogeneity. Western juniper cover and density in closed stands was as high as 90% and 1,731 trees ha⁻¹ on aspen sites or as low as 19% and 64 trees ha⁻¹ on low sagebrush sites (Table 3). The time

Table 6. Mean plant diversity indices within associations and subgroups for early and closed juniper woodlands. Hills diversity numbers: N0 = species number; N1 = Shannon's index, the number of abundant species; N2 = Simpson's index, the number of very abundant species. Neither mountain big sagebrush nor juniper cover were included in diversity indices.

Association	N0	N1	N2
Low sagebrush/Sandberg bluegrass			
open (n=5)	35	8.4	5.9
closed (n=4)	37	9.5	6.4
Mountain big sagebrush/ Thurber needlegrass			
open (n=5)	45	10.6	7.2
closed (n=6)	39	2.5	1.6
Idaho fescue (Devils Garden)			
open (n=6)	33	9.2	6.3
closed (n=9)	38	4.0	2.4
Idaho fescue (Steens Mt)			
open (n=9)	43	10.7	6.2
closed (n=6)	41	10.3	6.6
Quaking aspen			
open (9)	35	8.8	5.7
closed (4)	35	8.9	5.7

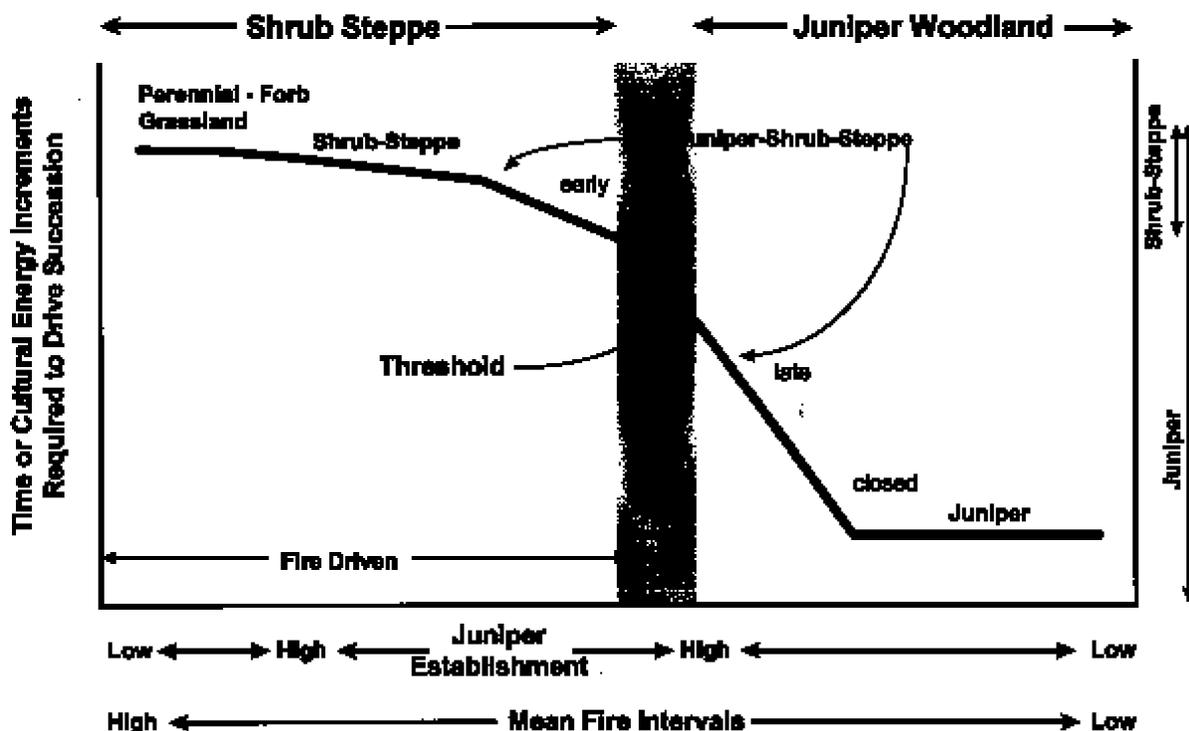


Fig. 6. Conceptual diagram of changes in a shrub steppe community in the absence of fire (modeled after Archer 1989). In the absence of fire the abundance of shrubs decline as juniper trees gain dominance. A threshold has been crossed when understory fuels drop to a level where fire is unlikely to carry through the stand or generate enough heat to kill trees > 3m tall. The probability of the woodland crossing the threshold and reverting back to shrub steppe is very low in the absence of a major disturbance or very costly inputs. Tree establishment declines due to a decrease in seed input and safe sites provided by shrubs.

required for woodlands to reach a closed state is highly variable. The minimum time required for woodlands to develop a closed canopy was 60 to 70 years in a mountain big sagebrush/Idaho fescue community (Miller and Rose 1999). Nearly 80% of the trees established within a 30 year period. Minimum time period for juniper stand closure to occur in an aspen stand was 80 years (Miller and Rose 1995). We typically observed less annual ring width in juniper stems during the early stages of woodland succession in aspen compared to mountain big sagebrush associations. Although these sites are generally more productive, interspecific competition among trees is probably greater.

Floristics and Diversity

We encountered 335 vascular plant species in our macro plots in the High Desert and Klamath Ecological Provinces. In pinyon-juniper woodlands across Nevada and Utah, West (1984) found 367 vascular plants species. In a more recent study, which included more sites and woodlands in southern Nevada (bordering the Mojave Desert), West et al. (1998)

reported nearly 500 species in pinyon juniper woodlands across Nevada. In our study, the contribution of perennial forbs was highly variable among and within associations and subgroups. Mean forb cover ranged between 1 and 16.5% among associations. On Steens Mountain, forbs accounted for a significant portion of the understory vegetation, while contributing 2% of the ground cover in northern California. Driscoll (1964) reported that forbs constituted a small portion of the understory in juniper woodlands in central Oregon. In open old growth western juniper woodlands in the pumice sand region of the Mazama Ecological Province (Fig. 1), perennial forb cover typically varied around 1% (Waichler et al. 2001).

The response of species diversity and richness to increasing juniper dominance varied among associations. During the transition from open to closed stands there was a decline in species number and richness in the mountain big sagebrush/Thurber needlegrass association, and a decline in richness in the mountain big sagebrush/Idaho fescue association in the Devils Garden area (Table 6). Removal of tree dominance in mountain big sagebrush/Thurber needlegrass association increased both species number and

richness (Bates et al. 2000). They reported 45 plant species in tree removal plots compared to 25 on adjacent closed woodland plots. In the pinyon-juniper region plant species richness is usually minimal in closed woodlands (West et al. 1978, 1998). However, juniper dominance appeared to have little effect on either species number or richness in the other associations we studied.

Management Implications and Conclusions

The identification of spatial and temporal heterogeneity in western juniper woodlands is extremely important when evaluating potential resource problems, assessing wildlife habitat values, and developing management plans. As shrub steppe communities are converted to juniper woodlands, community structure, composition, function, disturbance patterns, and wildlife habitat are altered. The conceptual model presented in Figure 6 (derived from Archer 1989) illustrates the conversion of a mountain big sagebrush steppe community to a juniper woodland in the absence

of fire. During the early phases of woodland development, transition is easily reversible with fire. By the mid to late stages of transition a threshold is crossed where the natural reversal to shrub steppe communities by fire is unlikely. As shrubs decline the probability of a fire intense enough to kill large juniper trees rapidly decreases. Juniper establishment declines with woodland maturity because of a decrease in seedling establishment sites as shrubs die out and an increase in intra-specific competition. On-site seed input also declines because of the loss of the fruit crop through increasing tree competition. As juniper woodlands close and mast crops and shrubs are lost (Miller and Rose 1995), fauna dependent on berries or shrubs also decline. Introduced weeds displacing native understory species represents a second potential threshold within this ecosystem. West (1999) separates juniper and pinyon systems into 2 phases: (1) trees do not dominate the open interspace where shrubs, grasses, and forbs control the microclimate and soils; and (2) trees dominate microclimates and soils across the major fraction of the matrix (including interspace). The threshold separating these 2 phases, savannas and woodlands, may be defined as the point where trees begin to influence the interspace causing changes in community structure (e.g. decline in shrubs) and community processes such as fire and water movement.

As community structure changes during woodland development, management options also change. Crossing an ecological threshold from shrub steppe to woodland not only results in a significant reduction in the role of fire, but depending on the site may result in the loss of native plant species and loss of soils. On the more arid sites in this study and in studies throughout the juniper and pinyon system, woodland development has led to desertification (West 1999) and reduction in site productivity (McDaniel and Graham 1992). Proper identification of the community and soils will indicate if the potential for these losses will be high or low with stand closure. In addition, the response of herbaceous understory to increasing juniper dominance may be influenced by past or current disturbance or the presence of introduced weeds. Structural characteristics described in Table 1 can help identify the woodland transitional state. Tree canopy cover and density alone are not of value if the maximum potential within an association has been defined.

In several of the plant associations we studied, the herbaceous understory cover remained intact as juniper dominance increased. This finding is counter to the results reported in much of the pinyon-juniper zone. However, the decline in understory we noted in the more arid big sagebrush associations is consistent with research from pinyon-juniper communities in Utah and Nevada (Arnold 1964, Blackburn and Tueller 1970, Meeuwig and Cooper 1981, Tausch et al. 1981, Everett and Sharrow 1985, Tausch and West 1995). Woodlands occupying more arid sites or soils with restrictive layers (e.g. petrocalcic or duric soil horizons) may be more prone to loss of understory. Both of these conditions may be similar to those found throughout the pinyon-juniper woodland alliance in the Intermountain Region. However, past and current overgrazing may also mask potential differences in herbaceous response to woodland development in the pinyon-juniper type. We and others (Dobrowolski, personal communication) have observed closed two needle pinyon-Utah juniper woodlands in Utah on moderately deep soils with perennial grass cover exceeding 10% cover. Identifying factors that help predict herbaceous response during woodland development should be a research priority. Based on our results, 2 initial hypotheses can be proposed: (1) sites with restrictive layers loose understory cover during woodland development, and (2) some understory dominants (in our case Thurber needlegrass) are poor competitors with juniper, and will decline during woodland development.

To reduce the confusion in both the literature and on environmental issues related to juniper and pinyon woodlands, the spatial and temporal heterogeneity of the site or landscape in question should be identified when conducting inventories, research, or developing management plans, and classification schemes.

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Long-term effects of fire on sage grouse habitat

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Abstract

This study documented the long-term (> 10 years) impact of fire on sage grouse (*Centrocercus urophasianus* Bonaparte) nesting and brood-rearing habitats on the Upper Snake River Plain in southeastern Idaho. The habitat of the study area is primarily mountain big sagebrush (*Artemisia tridentata vaseyana* Rydb.)—grassland. Twenty different-aged burns were sampled from 1996 to 1997, ranging from wildfires which burned during the 1960s to prescribed fires set during the 1990s. Canopy coverage and height of vegetation, and relative abundance of invertebrates, were estimated at burned and unburned sites within burns. Fourteen years after burning, sagebrush had not returned to pre-burn conditions. No difference was detected in forb abundance between different-aged burns. Relative abundance of ants and beetles was significantly greater in the 1-year old burn category but had returned to unburned levels by 3–5 years postburn. No benefits for sage grouse occurred as a result of burning sage grouse nesting and brood-rearing habitats. Burning created a long-term negative impact on nesting habitat because sagebrush required over 20 years of postburn growth for percent canopy cover to become sufficient for nesting.

Key Words: brood-rearing, *Centrocercus urophasianus*, nesting, sagebrush

Sage grouse (*Centrocercus urophasianus* Bonaparte) populations have declined across their entire range over the past 30 years (Connelly and Braun 1997). Sage grouse require sagebrush (*Artemisia* spp.) habitats at every stage of their life cycle (Patterson 1952) and the conversion of sagebrush rangeland to grassland for livestock grazing or for crop production has led to widespread loss, degradation, and fragmentation of sage grouse habitat (Braun et al. 1977). Currently, prescribed fire is a popular tool for removing sagebrush to increase forage production for livestock (Peterson 1995).

Several researchers studied short-term effects of fire on sage grouse habitat (Connelly et al. 1981, Gates 1985, Martin 1990, Benson et al. 1991, Robertson 1991, Fischer 1994), but no researcher has addressed longer-term (> 10 years) effects. During the first few years after burning, nesting habitat is essentially

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Resumen

Este estudio documenta el impacto a largo plazo (> 10 años) del fuego en los hábitats de anidamiento y crianza de polluelos de "Sage grouse" (*Centrocercus urophasianus* Bonaparte) en las planicies altas del río "Snake" en el sudeste de Idaho. El hábitat del área de estudio fue principalmente "Mountain big sagebrush" (*Artemisia tridentata vaseyana* Rydb.)—pastizal. De 1996 a 1997 se muestrearon 20 quemadas de diferente edad, variando de fuegos naturales que ocurrieron durante la década de 1960 hasta quemadas prescritas realizadas en la década de los 1990's. Se estimó la cobertura de la copa, la altura de la vegetación y la abundancia relativa de invertebrados en sitios quemados y no quemados dentro de las áreas incendiadas. 14 años después de la quema el "Sagebrush" no había regresado a las condiciones que se encontraba antes de la quema. No se detectaron diferencias en la abundancia de hierbas entre las áreas con diferente edad de quema. La abundancia relativa de hormigas y escarabajos fue significativamente mayor en las áreas con quemadas de 1 año de antigüedad y 3–5 años después la población de estos insectos regresó a los niveles existentes antes de la quema. La quema del hábitat de anidamiento y crianza de los polluelos "Sage grouse" no produce beneficio alguno para esta especie de ave. La quema produjo un impacto negativo a largo plazo en el hábitat de anidamiento porque el "sagebrush" requirió más de 20 años después de la quema para regenerar una cobertura de la copa suficiente para el anidamiento del "Sage Grouse".

destroyed and brood-rearing habitat is not improved. Prescribed burning may have different long-term effects as species diversity of vegetation and invertebrate food resources change with succession (Bendall 1974, Fischer et al. 1996), and could result in sub-optimal habitat for sage grouse.

We investigated the long-term impact of fire on sage grouse nesting and brood-rearing habitats in Clark and Fremont counties in southeastern Idaho. At least 186,694 ha of sagebrush were treated by prescribed burning, spraying, plowing, reseeded and burned by wildfires in Clark, Fremont and Jefferson counties from the 1950s through 1994. A prescribed burning program was instituted in the 1980s and removed 36,444 ha of sagebrush during the 1980s and 1990s, and wildfires (fires resulting from lightning strikes, humans accidentally or deliberately setting fires on private land that burned out of control), have burned 80,264 ha. Concurrently, the breeding population of migratory sage grouse in the study area declined significantly from the 1950s to the 1990s (Crowley and Connelly 1996).

Methods

Study Area and General Methods

The study area, in southeastern Idaho on the Upper Snake River Plain in Clark and Fremont counties, encompassed approximately 40,000 ha (44° 00' N, 111° 45' W). Ownership is divided among state, Bureau of Land Management, and private lands and includes parts of the Sand Creek Wildlife Management Area (WMA). Approximately 20,000 sheep and 1,660 cattle graze the area each year from May/June to September/October (G. Dawson, BLM, pers. comm.).

Mean spring and summer precipitation ranges from 20 cm on the southern end of the WMA to 46 cm in the north, and temperatures range from 4° C to 38° C during spring and summer (D. Aslett, IDFG, pers. comm.). Elevation ranges from approximately 1,430 m to buttes of 2,440 m (Crowley and Connelly 1996). Mountain big sagebrush (*Artemisia tridentata vaseyana* Rydb.) is the most common sagebrush subspecies, but three-tipped sagebrush (*A. tripartita* Rydb.) occurs as well. Other shrubs include bitterbrush (*Purshia tridentata* (Pursh) DC.), rabbitbrush (*Chrysothamnus* spp. Nutt.), and horsebrush (*Tetradymia canescens* DC.). Sand dunes in the southern end of the study area support stands of chokecherry (*Prunus virginiana* L.). A variety of grasses and forbs occur, including arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), tailcup lupine (*Lupinus caudatus* Kell.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), thick-spiked wheatgrass (*A. dasys - tachyum* (Hook) Scribn.) and Nevada bluegrass (*Poa nevadensis* Vasey) (Dalke et al. 1963).

By 1997, there were 8 wildfires and 12 prescribed burns in the study area (D. Aslett, IDFG, pers. comm., Crowley and Connelly 1996). Size and season of burn for the 4 oldest wildfires were not available, but mean size of 4 wildfires was 390 ha. Average size of 12 prescribed burns was 975 ha. We sampled the 20 burns from May through August during 1996 and 1997. Within unburned areas, vegetation was considered 37 years old; in burned sites, age of vegetation was based on time-since-burned. Vegetation was classified as unburned if there was no visible sign of fire (blackened stumps and blackened standing dead sagebrush) and no record of it having burned in the past 37 years. We sampled burns from 1 to 6 years old in both 1996 and 1997. All other burns were sampled in either 1996 or

1997, and the year in which they were sampled was determined randomly. Because of the mosaic nature of burns in sagebrush, we randomly sampled 4 times within each burn, twice in burned vegetation and twice in unburned vegetation. We sampled every site twice each field season, with approximately 1 month between samples, to incorporate variations in plant phenology and invertebrate abundance as the season progressed. At each site we laid a 50-m tape, oriented north-south, to mark the sampling transect.

Vegetation canopy cover and forb abundance

We measured percent shrub cover by species with the line intercept method (Canfield 1941), and at 5-m intervals along the transect, we measured grass height (cm) at the tape and the tallest sagebrush plant (cm) within 1-m radius of the tape. Forb composition and abundance were measured with a 2- x 5-dm frame (Daubenmire 1959), placed at 1-m intervals along the transect. We recorded the percent cover of grasses, litter and bare ground, and percent cover of the following forbs known to be important in the diet of sage grouse, associated with good brood-rearing habitat, or indicators of disturbance: western yarrow (*Achillea millefolium* L.), buckwheat (*Eriogonum* spp. Michx.), *Phlox* spp. L., false dandelion (*Agoseris glauca* (Pursh) Raf.), wild onion (*Allium* spp. L.), dandelion (*Taraxacum officinale* Weber), rosy pussytoes (*Antennaria rosea* Rydb.), death camas (*Zygadenus venenosus* Wats.), prickly pear (*Opuntia polyacantha* Haw.), sego lily (*Calochortus* spp. Pursh.), lupine (*Lupinus* spp.), prickly lettuce (*Lactuca serriola* L.), hawksbeard (*Crepis* spp. L.), common salsify (*Tragapogon* spp. L.), and prairie starflower (*Lithophragma* spp. Nutt.) (Klebenow and Gray 1968, Peterson 1970, Wallestad et al. 1975, Drut et al. 1994b, Pyle and Crawford 1996). We categorized these forbs as major forbs and other forbs encountered as miscellaneous forbs.

Relative invertebrate abundance

We used pitfall traps (modified from Fischer 1994) to sample the relative abundance of invertebrates within burns. Sixteen test tubes were sunk flush with the ground 50 cm apart in a 4 x 4 grid, located in a random direction 20 paces south of each vegetation transect. The test tubes were filled with a 1:1 solution of water and ethylene glycol and sealed with a cork until sampling began. During sampling, pitfalls were opened for 24 hours.

Invertebrates from all tubes at each grid were combined and stored in 70% alcohol. Invertebrates were separated into Hymenoptera (ants), Coleoptera (beetles), and Orthoptera (grasshoppers) in the laboratory, and all other invertebrates were categorized as miscellaneous. Samples were oven dried for 24 hours at 40° C, and weighed to 0.01g.

Statistical Analysis

We used SAS (SAS Inst., Inc. 1988) and SPSS (SPSS Inc. 1992) to analyze the data and considered differences significant if P

0.05. We transformed proportional data with the arcsine of the square root (Zar 1984) and plotted histograms to determine whether data were normally distributed. For univariate tests, we used the appropriate non-parametric test when data were non-normal. We were unable to determine whether or not vegetation had burned in areas categorized as burned by wildfire before the 1970s due to regrowth of vegetation. As a result we considered all vegetation from these sites as unburned. We pooled data between months and years for the prescribed burns from 1 to 6-years old that were sampled in both years, and pooled data between months for all other transects that were sampled in either year. This pooling resulted in a total of 84 transects, 38 which were from burned vegetation and 46 from unburned vegetation.

We used an exploratory cluster analysis (Hair et al. 1995) to produce a natural structure of vegetation characteristics based on a multivariate profile, including 10 variables known to be important in nesting and brood-rearing habitats (Dalke et al. 1963, Wallestad 1971, Peterson 1970) and/or strongly affected by fire (Bunting 1985, Wright 1985). These were: (1) percent sagebrush cover, (2) percent bitterbrush cover, (3) percent cover of standing dead shrubs, (4) percent total live shrub cover, (5) sagebrush height in cm, (6) grass height in cm, (7) percent grass cover, (8) percent litter cover, (9) percent cover of major forbs, and (10) percent cover of miscellaneous forbs. The number of clusters chosen from the cluster analysis for use in subsequent analyses was based on the minimum number of clusters that were characterized by identifiable and useful (from a management perspective) vegetation age categories.

We used a confirmatory MANOVA (Hair et al. 1995) to establish that clusters were statistically distinct and report the P values as descriptive measures of these differences. We used a Kruskal-Wallis one-way analysis of variance (Zar 1984)

Table 1. Characteristics of different-aged burn clusters from the Upper Snake River Plain, SE Idaho, 1996–1997.

Variable	Cluster									
	1-year old burn		3 to 5-year old burns		6 to 14-year old burns		Low elevation		Unburned vegetation	
	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
Elevation (m) ¹	1698 ^a	239	1728 ^a	4310	1759 ^a	10928	1623 ^b	7861	1730 ^a	7643
Sagebrush (%)	0 ^a	0	0 ^a	0	8 ^b	32	12 ^{bc}	27	18 ^c	58
Total shrub (%)	0 ^a	0	10 ^b	17	16 ^{bc}	45	19 ^c	27	35 ^d	63
Sagebrush height (cm)	9 ^a	127	11 ^a	33	49 ^b	121	63 ^c	43	71 ^c	55
Grass (%)	25 ^a	159	48 ^b	160	33 ^a	82	65 ^b	72	34 ^a	102
Litter (%)	68 ^a	33	84 ^b	5	82 ^b	13	86 ^b	2	83 ^b	85
Bitterbrush (%)	0 ^a	0	7 ^{bc}	22	6 ^{ab}	31	5 ^{ab}	43	16 ^c	83
Standing dead shrub (%)	2 ^a	3	5 ^{ab}	8	3 ^a	5	6 ^{ab}	28	6 ^b	12
Miscellaneous forbs (%)	10 ^a	22	17 ^a	114	15 ^a	97	13 ^a	29	12 ^a	35
Major forbs (%)	11 ^a	5	15 ^a	13	15 ^a	42	12 ^a	6	14 ^a	23
Grass height (cm)	17 ^a	13	26 ^a	13	19 ^a	36	26 ^a	50	24 ^a	44

¹Within row means significantly different at $\alpha = 0.05$ have different letters.

to test whether the 6 forbs identified in the literature as the most important food items in sage grouse diet (common yarrow, sego lily, hawksbeard, prickly lettuce, dandelion and yellow salsify) (Peterson 1970, Wallestad et al. 1975) differed in abundance among different-aged burns.

We used the same grouping of transects suggested by the vegetation cluster analysis to analyze the invertebrate data and used a MANOVA (Hair et al. 1995) to test if relative invertebrate abundance differed among different-aged burns. In both MANOVA's we used Pillai's trace statistic as the test statistic, Tukey's multiple comparison test (Zar 1984) for post-hoc comparisons, and a canonical analysis (Hair et al. 1995) to determine which variables were most important in separating clusters.

Results

Cluster composition

We selected 5 clusters for analyses and excluded 1 transect that did not enter a cluster. We described clusters according to the age of the majority of the vegetation in each cluster. Four relatively distinct age classes emerged, although clusters included transects from burns older or younger than the age class used to identify the cluster. One cluster was difficult to describe with respect to vegetation age and other criteria, such as elevation and soil, were used to characterize it.

The first cluster (n = 5) contained characteristic post-disturbance vegetation, with an absence of shrub cover and an increase in canopy cover of aggressive colonizers such as the dandelion tribe (*Taraxacum officinale* and *Agoseris* spp.). Four of the 5 transects were from 1-year old burns and the remaining transect was from a 14-year old burn. The second cluster (n = 9) was

representative of an early seral stage. Facultative seral species such as western yarrow and rosy pussytoes had increased in canopy cover, and bitterbrush had begun to return. Eight transects came from burns ranging from 3 to 5-years old, and the remaining transect was from a 27-year old burn. The third cluster (n = 16) contained 11 vegetation transects ranging from 6 to 14-years old, and was representative of mid-seral vegetation. Sagebrush had begun to contribute to the shrub cover, there was a decrease in canopy cover of some early seral stage forbs, such as dandelion, false dandelion and western yarrow, and forbs typically damaged by fire, such as *Eriogonum*, had increased in canopy cover. This group also contained 3 transects from unburned vegetation 36 years old, and 2 transects from younger burns (4 and 5 years old). The largest cluster (n = 48) comprised 40 unburned vegetation transects 36 to 37-years old and was representative of late seral vegetation, with sagebrush and bitterbrush at their greatest canopy cover. Within this cluster 8 transects were from burned vegetation 12 to 27-years old. The last cluster (n = 5) contained 2 unburned vegetation transects 36 years old, 2 transects from 10-year old burns, and 1 transect from a 16-year old burn. This cluster was difficult to characterize by vegetation age, but all transects were from the lowest elevations sampled. These 5 transects also had very sandy soil, were heavily grazed by cattle and sheep, and were some of the most southerly and westerly sites sampled. In total, 73 (88%) of 83 transects clustered as expected based on years since burned.

Effect of time-since-burned on vegetation

Vegetation characteristics differed ($F = 8.95$, $P = 0.0001$) among burns based on

the 10 variables selected for the cluster analysis, plus elevation. The first canonical variable described 80% of the variation in the data. Sagebrush height and percent canopy cover, percent total shrub cover, and percent grass cover were primarily responsible for the separation of clusters with canonical coefficients of 1.82, 0.72, 0.65, and -0.58, respectively. The absolute value of all other canonical coefficients was < 0.39. Percent grass cover was inversely related to sagebrush height and cover and to total shrub cover.

All variables in the univariate tests differed ($P < 0.05$) among the 5 vegetation clusters, except for percent cover of the major and miscellaneous forbs and grass height (Table 1). Sagebrush canopy cover was less in 1-year old burns, 3 to 5-year old burns and 6 to 14-year old burns than in unburned vegetation. Low elevation sites did not differ in sagebrush canopy cover from unburned vegetation and 6 to 14-year old burns but had more sagebrush than younger aged burns. Total shrub cover was greater in unburned vegetation than in all other clusters, and unburned vegetation had taller sagebrush shrubs compared with all other clusters except the low elevation sites. The 1-year old burns and 3 to 5-year old burns did not differ in sagebrush shrub height, but both had smaller sagebrush shrubs than 6 to 14-year old burns.

Grass cover in 3 to 5-year old burns and low elevation sites was greater than grass cover in 1-year old burns, 6 to 14-year old burns and unburned vegetation, among which there was no difference in grass cover. Litter cover did not differ among clusters, except in 1-year old burns which was lower compared to all other clusters.

Bitterbrush canopy cover was less in 1-year old burns compared with 3 to 5-year old burns and unburned vegetation. Unburned vegetation had more bitterbrush

Table 2. Composition of major sage grouse food forbs in different-aged burn clusters, Upper Snake River Plain, SE Idaho, 1996–1997.

Forb genera	1-year old burn	3 to 5-year old burns	6 to 14-year old burns	Low elevation	Unburned	P
Achillea	0.57 ¹	1.73	1.08	0.84	1.12	0.11
Calochortus	0	0	0	0.51	0	0.28
Crepis	0	0	0.53	0.51	0.52	0.23
Lactuca	0	0.54	0.69	0.57	0.57	0.41
Taraxacum	1.47	1.18	0.84	1.63	0.76	0.07
Tragopogon	0.68	0.57	0.59	0.93	0.58	0.06

¹Mean percent canopy cover of each forb in different-aged burn clusters.

than other clusters, except burns from 3 to 5-years old. However, this is probably a result of high variance in 3 to 5-year old sites and unburned sites. The 1-year old burns and 6 to 14-year old burns had less standing dead shrub cover than unburned vegetation.

The abundance of major and miscellaneous forbs was similar among clusters (Table 1). Major food items, common yarrow, lily, hawksbeard, prickly lettuce, dandelion and yellow salsify, did not differ in abundance among different-aged burns (Table 2).

Effect of time-since-burned on invertebrate relative abundance

Relative abundance of invertebrates, measured as dry weight in grams, differed among vegetation age clusters ($F = 3.16$, $P = 0.001$), and we rejected the null hypothesis that there was no effect of time-since-burned on invertebrate abundance. A canonical analysis revealed that relative abundance of beetles was most influential in separating clusters. In univariate tests, relative abundance of ants and beetles differed among vegetation age clusters (Table 3). There were significantly more beetles in 1-year old burns than in all other age clusters. The 1-year old burns also contained more ants than 3 to 5-year old burns and unburned vegetation, but there was no difference in the relative abundance of grasshoppers or miscellaneous invertebrates among different-aged burns.

Discussion

Response of vegetation to fire can vary considerably because of differences in topography, slope, fine fuel load, moisture content of vegetation, fire intensity, season of burn and postburn climatic conditions (Daubenmire 1968, Winward 1985). Inherent variation in vegetation responses to burning can render predicting the long-term effects of fire difficult. Ten transects were not clustered as expected based on years since burned. This finding possibly resulted from variations in vegetation due to topography, grazing pressure, post-climatic conditions or fire intensity. For example, transects from young burns clustered with older burns may have been due to rapid recovery from low-severity fires. Transects from older burns clustered with younger burns could be a result of heavy grazing pressure. Despite many factors contributing to variable responses of vegetation to fire, some clear long-term effects of fire upon sage grouse habitat were detected on the Upper Snake River Plain.

Except for occasional sprouting by threetip and silver sage (*A. cana*, which was not present within the study area), sagebrush species are nonsprouters and are easily killed by fire (Tisdale and Hironaka 1981, Blaisdell et al. 1982). Although sagebrush was beginning to re-establish in 6 to 14-year old burns on the Upper Snake River Plain, mean sagebrush canopy cover 14 years postburn was less than one-half that of unburned vegetation and mean

sagebrush height was 69% of unburned vegetation. In general, mountain big sagebrush usually re-establishes within 5 to 10 years (Winward 1985), and may return to preburn density and cover within 15 to 20 years postburn (Bunting et al. 1987). However, severe fires can slow re-establishment, so that sagebrush takes longer to recover and dominate an area (Bunting et al. 1987). This factor may explain why sagebrush in many burns on the Upper Snake River Plain took relatively longer to return to preburn levels. After a severe fire on the US Sheep Experimental Station in southeastern Idaho, 30 years passed before sagebrush was once again the dominant species (Blaisdell et al. 1982).

Eighty-six percent of transects from 36-year old burns were clustered with unburned vegetation, suggesting that 36 years is sufficient time to recover. Our ability to more precisely define how long vegetation takes to return to preburn conditions on the Upper Snake River Plain was limited by the lack of burns 20 to 30 years old. Even though 3 of the 4 transects from fires between 20 and 30 years old were clustered with unburned vegetation, it is not possible to conclude that this is sufficient time for all burned areas to return to preburn conditions. These 3 transects may have recovered sooner than average due to other influences, such as being lightly burned and/or having favorable postburn climatic conditions. Information from burn reports provided little help in resolving these questions.

Removing the shrub component through fire may allow grasses and forbs to increase in productivity and abundance. In general, total herbage production of grasses reaches a maximum 2 to 5 years after burning, after which it declines as sagebrush and other shrub species increase (Blaisdell et al. 1982, Bunting 1985). In short-term studies, Martin (1990) found significantly more grass cover 2 years postburn, but Pyle and Crawford (1996) reported a significant reduction in total grass cover 1 year postburn, and no differ-

Table 3. Dry weight of invertebrates in different-aged burn clusters, Upper Snake River Plain, SE Idaho, 1996–1997.

Variable	Cluster									
	1-year old burn (n=5)		3 to 5-year old burns (n=9)		6 to 14-year old burns (n=16)		Low elevation (n=5)		Unburned vegetation (n=48)	
	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance	Mean	Variance
	(g)		(g)		(g)		(g)		(g)	
Ants ¹	0.46 ^a	0.40	0.08 ^b	0.01	0.15 ^{ab}	0.07	0.25 ^{ab}	0.09	0.09 ^b	0.02
Beetles	1.7 ^a	1.36	0.39 ^b	0.02	0.42 ^b	0.08	0.73 ^b	0.13	0.54 ^b	0.13
Grasshoppers	0.81 ^a	0.58	0.28 ^a	0.05	1.22 ^a	8.1	0.13 ^a	0.02	0.42 ^a	0.83
Miscellaneous	0.02 ^a	0.00	0.09 ^a	0.00	0.05 ^a	0.04	0.07 ^a	0.00	0.07 ^a	0.01

¹Within row means significantly different at $\alpha = 0.05$ have different letters.

ence between treatment and controls 2 years postburn. Grass cover on the Upper Snake River Plain was greatest in 3 to 5-year old burns, which had very sparse shrub cover and had returned to preburn levels by 6 to 14 years postburn as the shrub canopy cover increased.

Height and canopy cover of sagebrush and grass are important characteristics of sage grouse nest sites. Sage grouse need a minimum of 15% overall sagebrush canopy cover for successful nesting (Wallestad and Pyrah 1974). Height of nest shrubs ranges from 36 cm to 70 cm (Patterson 1952, Wallestad and Pyrah 1974, Rothenmaier 1979, Wakkinen 1990, Sveum et al. 1998), and sagebrush canopy cover at nests ranges from 15 to 40% (Klebenow 1969, Wallestad and Pyrah 1974, Braun et al. 1977, Rothenmaier 1979). Sagebrush canopy cover measured within a 1-m² plot at nest sites averaged 51% and 59% in a 2 year study in Washington by Sveum et al. (1998). Only unburned vegetation on the Upper Snake River Plain offered both sagebrush height and cover within the range of conditions most frequently used for nesting as reported in the literature. Sagebrush height was within the range used by nesting grouse by 6 to 14 years postburn, but sagebrush canopy cover (only 8%) was insufficient for nesting. Insufficient sagebrush canopy cover may result in hens nesting under other shrub species. Hens have been found nesting under non-sagebrush shrubs (e.g. snowberry (*Symphoricarpos oreophilus* Gray), bitterbrush, rabbitbrush), but nesting success was lower compared to birds nesting under sagebrush (Connelly et al. 1991). Compared with the 20% to 40% total shrub canopy cover used by sage grouse (Braun et al. 1977), total shrub canopy cover in burns up to 14 years old on the Upper Snake River Plain did not provide adequate canopy for nesting.

Grass height and percent grass cover adequate for nesting occurred in nearly all burn clusters. Mean grass height at nests was reported at 19 cm (Wakkinen 1990, Connelly et al. 1991). Only 1-year old burns failed to provide sufficiently tall grass. Grass cover measured at nest sites ranges from 3.7% to 27% (Klebenow 1969, Wakkinen 1990, Connelly et al. 1991, Musil et al. 1994, Sveum et al. 1998), and percent grass cover in all burn clusters provided as much, or more, cover.

Brood-rearing occurs in a wide range of shrub heights and densities. Shrub heights at brood locations range from 15 to 37 cm (Martin 1970, Wallestad 1971). Sagebrush canopy cover ranges from 6% to 31% for

feeding during the day (Klebenow 1969, Peterson 1970, Martin 1970, Wallestad 1971, Klott and Lindzey 1990), to denser cover and taller shrubs at night for roosting (Dunn and Braun 1986). Burns > 5-years old on the Upper Snake River Plain provided shrubs of height and density within the range of conditions used by broods. While mean sagebrush heights in 6 to 14-year old burns and unburned vegetation may exceed 37 cm, the variance of sagebrush heights in these clusters was large (Table 1), indicating that sagebrush of preferred heights occurred.

Brood-rearing habitat must provide forbs and insects for food. Total forb cover in the different-aged burns on the Upper Snake River Plain fell within or exceeded values reported in the literature as preferred brood-rearing habitat, ranging from 12 to 14% (Drut et al. 1994a) to 17% (Klott and Lindsey 1990) to 22% (Wallestad 1971). The abundance of major forbs and average grass height in the understory of unburned vegetation was similar to burned vegetation, and the increase in grass cover in burned vegetation was short-lived. In general, total herbage production of forbs reached a maximum 2 to 5 years postburn, after which it declined as sagebrush and other shrubs increased (Bunting 1985). Perennial forb cover, total forb cover, and total forb diversity increased during the second growing season after a fire in Oregon (Pyle and Crawford 1996), and forbs increased the first 2 years post fire in eastern Idaho (Martin 1990). Harniss and Murray (1973) found that forbs on burned plots maintained a greater biomass for 5 to 15 years after burning compared to control plots.

In contrast to the above studies, no significant difference in forb cover was detected among different-aged burns on the Upper Snake River Plain. This finding is similar to what Fischer et al. (1996) reported from a study of the effects of fire in the Wyoming sagebrush (*A. tridentata wyomingensis* Nutt.) habitat in southeastern Idaho, where forb cover was similar in burned and unburned habitat up to 3 years postburn. Fischer et al. (1996) concluded that drought conditions might have limited forb response to reduced shrub competition. The Upper Snake River Plain region also experienced drought conditions throughout much of the 1980s and early 1990s (D. Aslett, IDFG, pers. comm.). Approximately 7,900 sheep graze the 3 to 5-year old burns from May/June through September/October each year (Greg Dawson, BLM, pers. comm.), and livestock may remove enough forb biomass so that postburn response was not detectable. The lack of forb response

could be a combination of drought and livestock grazing (Coggins 1998).

Invertebrates are essential in the diet of sage grouse chicks (Patterson 1952, Klebenow and Gray 1968, Peterson 1970), and the amount of insects consumed is positively correlated with chick survival and growth (Johnson and Boyce 1990). We found no long-term effect of fire on invertebrate abundance. However, Fischer et al. (1996) found significantly fewer ants 2 to 3 years postburn in burned compared with unburned vegetation. The increase in Coleopteran abundance 1-year postburn on the Upper Snake River Plain has not been reported in other studies (Fischer et al. 1996, Pyle and Crawford 1996), although Rickard (1970) found that some Coleopteran species were less abundant in burned habitat compared with unburned habitat. The initial increase in ant and beetle abundance after a fire observed on the Upper Snake River Plain may be of limited value to sage grouse chicks because most shrub cover was removed, potentially increasing chick vulnerability to predation when foraging in open areas.

Conclusions and Management Implications

Burning to remove sagebrush on the Upper Snake River Plain is not justifiable as a sage grouse management practice because only unburned vegetation in the area offers suitable nesting habitat. No brush control work should occur where live sagebrush cover is less than 20% (Braun et al. 1977), as it is in unburned vegetation on the Upper Snake River Plain.

Each burn may seem inconsequential in relation to the entire area of sagebrush habitat apparently available to sage grouse on the Upper Snake River Plain. However, the cumulative effect of burning upon critical nesting and brood-rearing habitats could be seriously detrimental to a sage grouse population if vegetation over a large area remains in sub-optimal conditions for many years. From 1980 through 1996, 11,676 ha were burned by prescribed fire, which accounted for approximately 29% of the study area, none of which is currently suitable nesting habitat and much of which is not good brood-rearing habitat. Many of these burns are juxtaposed to create large contiguous areas of sub-optimal nesting habitat. Burn programs should be planned to avoid creating a landscape of adjacent young burns, especially of burns younger than 14-years old. Future research should involve mapping the

pattern of burned/unburned sagebrush on the Upper Snake River Plain to better plan and implement future prescribed burns.

Scheduling when a habitat is burned should not be predetermined by the length of time since the area last burned. Although other studies suggest that sagebrush returns to preburn conditions by 15 years postburn (Bunting et al. 1987), our results demonstrate that this is not the case for sagebrush in the Upper Snake River Plain. By measuring 3 variables (sagebrush height, percent sagebrush canopy cover and percent total shrub cover) at permanent, randomly located transects within burned vegetation, a fast and efficient monitoring program to follow the recovery of vegetation could be implemented. The recovery of burned vegetation with respect to sage grouse nesting and brood-rearing requirements could then be evaluated.

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Suppression of grasshoppers in the Great Plains through grazing management

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Abstract

It was hypothesized that grazing management could mitigate grasshopper outbreaks on native rangeland in the northern Great Plains. Key practices would require deliberate variation in timing and intensity of grazing events, preservation of canopy during critical periods of grasshopper development, and reductions in areas of bare soil. The twice-over rotational grazing system appeared compatible with those requirements.

Grasshopper population trends were monitored during 1993–1995 and 1997–1998 on commercial native rangeland under twice-over rotational grazing vs traditional season-long grazing. A ubiquitous pest grasshopper, *Melanoplus sanguinipes* (Fabricius), occurred at every sample site during each year in numbers sufficient to provide life history parameters for comparison between treatments. Under rotational grazing, the nymphs developed significantly slower and their stage-specific survival rates were significantly lower and less variable. Consequently, significantly fewer adults were produced significantly later in the season under rotational grazing.

Seasonal presence of all grasshopper species combined averaged 3.3X higher under season-long grazing than under rotational grazing. Local outbreaks that generated 18 and 27 adult grasshoppers per m² under season-long grazing in 1997 and 1998, respectively, did not occur under rotational grazing. The outbreaks consumed 91% and 168%, respectively, as much forage as had been allocated for livestock, as opposed to 10% and 23%, respectively, under rotational grazing.

Of 9 important grasshopper species, none were significantly more abundant at rotational sites than at season-long sites. Three species that were primary contributors to outbreaks under season-long grazing remained innocuous under rotational grazing. It therefore appears that outbreak suppression through grazing management is feasible in the northern Great Plains.

Key Words: grasshopper management, twice-over grazing system, rotational grazing, *Melanoplus sanguinipes*

In a study of statistical density dependence among rangeland grasshoppers in Montana, Kemp and Dennis (1993) reported equilibrium or "return tendency" parameters for populations in 3 regions of the state; northern plains, southern plains, and western mountains. Long-term median (5.3, 5.4, 4.8 m⁻²) and mean (6.1, 6.2, 6.3 m⁻²) densities of adult grasshoppers were similar for the

Resumen

Hipotizamos que el manejo del apacentamiento podría mitigar los brotes de chapulines en los pastizales de las Grandes Planicies del Norte. Prácticas clave podrían requerir la variación deliberada en tiempo e intensidad de los eventos de apacentamiento, la preservación de la copa durante los periodos críticos del desarrollo de los chapulines y la reducción de áreas de suelo desnudo. El sistema rotacional doble parece ser compatible con esos requerimientos.

Las tendencias de la población de chapulines se monitorearon de 1993 a 1995 y de 1997 a 1998 en pastizales nativos comerciales manejados bajo los sistemas de apacentamiento rotacional doble rotación y el sistema tradicional de apacentamiento estacional. En todos los sitios experimentales cada año se tuvo plaga de chapulines [*Melanoplus sanguinipes* (Fabricius)] en número suficiente para proveer los parámetros del historial de vida utilizados para comparar los tratamientos. Bajo el sistema de apacentamiento rotacional el desarrollo de las ninfas fue significativamente más lento y las tasas de sobrevivencia en estados específicos fueron significativamente menores y menos variables. Consecuentemente, con el sistema rotacional la producción de adultos fue significativamente más baja y los adultos se produjeron significativamente más tarde.

La presencia estacional de la combinación de todas las especies de chapulines promedio 3.3 veces más en el sistema de apacentamiento estacional que en el rotacional. Los brotes locales de 1997 y 1998 produjeron 18 y 27 chapulines adultos por m² bajo el sistema estacional y estos brotes no ocurrieron con el sistema de apacentamiento rotacional. Los brotes de chapulines consumieron el 91 y 168% del forraje que había sido asignado para el ganado, en tanto que en el sistema rotacional el consumo fue del 10 y 23% respectivamente.

De 9 especies importantes de chapulines ninguna fue significativamente más abundante que otra en ambos sistemas de apacentamiento. Tres especies que fueron las principales en los brotes ocurridos en el sistema estacional permanecieron inocuas bajo el sistema rotacional. Por lo tanto, parece que en la región de las Grandes Planicies del Norte la supresión de brotes de chapulines es factible mediante el manejo del apacentamiento.

respective regions. However, estimated regional carrying capacities were much higher for the 2 plains regions than for the mountains (8.9 and 8.6 vs 6.3 m⁻², respectively). Consequently, grasshopper populations were much more variable in the plains, and grossly over-shot the carrying capacity (i.e., reached outbreak levels) much more frequently than in the mountains. These results provided useful insights for assessing opportunities for

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long-term grasshopper management in the northern Great Plains.

Whether ranch managers realize it or not, the effects of long-term mean or median grasshopper populations have been factored into historical livestock carrying capacities in the northern Great Plains. Total forage consumption by grasshoppers plus livestock usually does not exceed intended levels, but grasshoppers far exceed normal consumption during outbreaks. Therefore, a goal of grasshopper management could be to reduce either the frequency, the severity, or the duration of an outbreak. A viable approach might be to reduce grasshopper carrying capacity by making the rangeland environment less hospitable for these pests.

Grazing Management and Grasshopper Outbreaks

In several Great Plains ecosystems, grasshoppers tend to achieve highest densities in the presence of grazing during years of low precipitation and low forage production. Grasshoppers have been reported to be unusually abundant during dry seasons in heavily grazed pastures of mixed grass prairie in Oklahoma (Smith 1940), tall grass prairie in Kansas (Campbell et al. 1974), unspecified habitat in eastern Montana (Pepper 1955), and fescue grassland in Alberta (Holmes et al. 1979). In eastern Montana, grasshopper populations were inversely proportional to plant canopy height, and highest infestations occurred where ground cover was less than 40% (Anderson 1964). These reports provided primarily qualitative descriptions of relationships, but some quantification can be extracted from other data for Montana. Kemp (1992) reported long-term grasshopper density data for eastern Montana rangeland, and Kemp and Cigliano (1994) reported long-term drought index data for the same region. During 19 seasons for which data on both variables were available, above-average grasshopper densities occurred 1 year out of 8 in the absence of drought, but occurred 7 years out of 11 in the presence of drought. Thus, there is little doubt that the greatest demand for available forage in eastern Montana occurred during seasons when ranchers could least afford to feed grasshoppers.

A modeling exercise by Onsager (1983) suggested that density levels and forage destruction rates by the migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), were most sensitive to

changes in survival rate and development rate. In field tests, Grant et al. (1993) determined that rates of mortality, nymphal development, and egg production were, in that order, the 3 most important determinants of population fitness. Thus, successful management would likely have to impair at least one of those functions.

In a discussion of potential tactics for proactive grasshopper management, Onsager (1995) dismissed traditional season-long grazing as offering little opportunity. Periodic grasshopper outbreaks of the past have occurred predominantly under season-long grazing, and the species involved are now cited as classic examples of obnoxious pests. In contrast to season-long grazing, deferment or rotation of grazing periods can deliberately manipulate the time, rate, or degree of defoliation, which in turn might be strategically useful in influencing the time, rate, degree, or direction of change in habitat for grasshoppers. The latter strategies also may prevent repetitively favoring the same pest species in the same pasture for consecutive seasons.

Anderson's (1964) report of high infestations associated with low ground cover also provided a useful, testable hypothesis. Two pest species ranked among the 5 worst by Dysart (1995), *Aulocara ellioti* (Thomas) and *Ageneotettix deorum* (Scudder), are known to deposit their egg-pods horizontally in small patches of bare soil, just below the surface (Anderson and Hastings 1966, Onsager 1963), where heat accumulation is maximized (Pierson and Wight 1991). This promotes a well-synchronized hatch that is completed relatively early in the season (Fisher 1994), and the young nymphs accommodate relatively cool temperatures by basking in the bare patches with their bodies perpendicular to sunlight and in contact with the warm soil. Reducing the size and frequency of bare spots should reduce densities of those 2 species and perhaps slow down the development rate of other species as well.

Consolidation of the preceding considerations yielded 3 hypothetical attributes of a grazing system that might deter (or, at least, fail to encourage) grasshopper outbreaks in the northern Great Plains. These were; (1) deliberate variation from year to year in the time and intensity of defoliation periods, (2) controllable preservation or enhancement of shading canopy during critical portions of grasshopper life cycles, and (3) reduction or elimination of bare soil. The twice-over rotational grazing system appeared to be compatible with those requirements.

The twice-over rotational grazing strategy was described in detail by Manske (1994a) and Biondini and Manske (1996). From the perspective of hypothetical beneficial attributes for grasshopper management, it can be described briefly as follows. It requires 2 sequential rotations of a herd of livestock through a series of 3 to 6 pastures within a 4.5-month grazing season. In the northern Great Plains, the first grazing cycle occurs 1 June to 15 July. This grazing cycle tends to distribute defoliation over a higher proportion of plants and tends to leave a more level canopy than typically occurs when the herd has continuous access to the same total area during the same period of time. During the interval between the 2 grazing periods within each pasture, new tillers proliferate and tend to fill in the bare spots. The canopy produces relatively few reproductive stems, so it tends to remain relatively level while it grows in height. The second grazing cycle occurs 16 July to 15 October, when pastures are grazed for a second time, in the same sequence as for the first time, for twice as many days as they were grazed during the first cycle. The second cycle also appears to promote more uniform harvest than typically seen under season-long grazing. That may have an important impact on soil temperatures, grasshopper basking efficiency, and grasshopper egg development rates, because less soil is exposed to direct sunlight for a shorter time than under season-long grazing. The exit pasture becomes the entry pasture for the next season, but otherwise the same sequence of pasture use is retained from year to year, which assures that periods of pasture usage are systematically changed each year. That could reduce the probability that any given pest grasshopper species will be inadvertently favored for successive generations in any given pasture.

Materials and Methods

The Study Area

The experimental area was 34 km west of Watford City, N.D., between 47°35' to 47°50' N Lat and 104°00' to 103°45' W Long, within the McKenzie County Grazing District of the Little Missouri National Grasslands. The forage base is predominantly native prairie comprised of blue grama [*Bouteloua gracilis* (HBK.) Lag. ex Griffiths], western wheatgrass (*Agropyron smithii* Rydb.), needle-and-thread (*Stipa comata* Trim. & Rupr.), and threadleaf sedge (*Carex filifolia* Nutt.),

interspersed with patches that had been planted to crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] in the 1930s (Uresk and Bjugstad 1995).

A total of 9 study sites were established in 2 grazing allotments that utilized different grazing strategies. The first allotment was comprised of 5 pastures. One pasture was predominantly crested wheatgrass that was always grazed from 1 May to 31 May (grazing after 15 October also was an option); it had 2 study sites. The other 4 pastures were native prairie that had since 1989 been under twice-over rotational grazing from 1 June to 15 October. Each of the 4 pastures had 1 study site. The second allotment was a single large pasture of predominantly native prairie with interspersed patches of crested wheatgrass. It was grazed season-long from 1 May to 15 September and had 2 study sites on native prairie plus 1 in a patch of crested wheatgrass. The 4 study sites within native rotational pastures were selected because the lessee had been using them for annual photographic monitoring purposes since 1989. The other 5 study sites were selected by Manske (1993) as typical representatives of their respective pastures. The native prairie rotational pastures comprised a total of 1,780 ha with a preference stocking rate of 0.872 AUM ha⁻¹ and a 4.5-month grazing period. The season-long pasture was 8,500 ha with a preference stocking rate of 0.862 AUM ha⁻¹ and a 4.5-month grazing period. The permitted stocking rate for all pastures was set by the US Forest Service at 100% of preference levels in 1993–1997, and at 90% of preference levels in 1998.

Sampling Procedures

To support grasshopper density sampling via the method of Onsager and Henry (1977), each study site was provided with a set of 40 aluminum wire rings, each 0.1m², affixed for the duration of the study (1993–1998) in a 4x10 array with 8 m between rings. For the first 2 seasons of the study, Manske (1993, 1994b, 1994c) periodically determined percent basal cover, percent bare ground, and total above-ground biomass at all sites. Each site also was equipped with a 5.8-m² x 1.2-m-high wire-mesh stock panel enclosure to protect an instrument shelter and weather monitoring equipment. In 1994 and 1998, Omnidata® Datapods were used to record daily minimum and maximum temperature at 5 cm below and 15 cm above the soil surface.

Grasshopper populations were sampled at varying intervals for 5 seasons,

1993–1995 and 1997–1998. Sampling began as soon as sites were accessible in the spring and terminated after killing frosts in the fall. Total density was estimated by counting grasshoppers within each ring of an array (i.e., in a total area of 4 m²), and a sweep net collection was taken along the perimeter of the array to establish composition of the population by species and by stage of development. Thereafter, an index of seasonal abundance called "grasshopper days" (GD) theoretically could be determined for any stage of any species at any site by calculating the area under a graph of density plotted as a function of time expressed in days (Hewitt and Onsager 1982). In practice, however, the sampling method is not reliable for very small grasshoppers, and during every season, some early-hatching species began development before the first sampling event. Therefore, GD values were calculated only for 3rd instar or older stages. In concept, a GD differs from an AUM only in that the herbivores are smaller and the time units are shorter.

Study sites were sampled at 7-to 10-day intervals during 1993, 1995, and 1998, and at 2-to 3-day intervals during 1994 and 1997. That intensity of sampling supported estimation of certain stage-specific life history parameters for at least the more abundant species at all study sites. The parameters that were considered important in this study were average stage-specific survival rates for 3rd, 4th, and 5th nymphal instars, average development time per nymphal instar, average daily survival rate for both nymphs and adults, and the number of individuals that entered the adult stage. The mathematical procedure, which combined methods of Richards et al (1960), Kiritani and Nakasuji (1967), Manley (1976), and Onsager and Hewitt (1982a), was described in detail by Sanchez and Onsager (1988).

Statistical Analyses

Because of occasional instrument malfunction, the weather records from within grazing enclosures in 1994 and 1998, respectively, provided 5 and 3 natural time intervals that ranged from 11 to 38 days in duration when continuous data were available from each study site. For each of the 2 years, soil temperatures within each continuous time interval were converted to cumulative degree-days over 10°C, the temperature used by Kemp and Sanchez (1987) as a threshold for modeling grasshopper egg development. Air temperatures were similarly converted to cumula-

tive degree-days over 17.8°C, a threshold for nymphal development (Putnam 1963). For each season, the degree-day data were subjected to an analysis of variance as a randomized complete block design with the 9 study sites handled as treatments and the intervals considered replications over time.

For routine exploratory analyses of grasshopper population or life history parameters, the basic statistical design was a 2x2 factorial of 4 grazing treatments comprised of 2 vegetation types, crested wheatgrass and native prairie, exposed to 2 methods of grazing, twice-over rotational and season-long. Each season was considered a replication in time. The treatment by season interaction was the error term. Data from different sites within the same treatment and year were considered subsamples. Treatment and error variances were partitioned into 3 orthogonal comparisons: (1) all crested wheatgrass sites vs all native prairie sites; (2) crested wheatgrass sites used for spring pasture in support of twice-over rotational grazing vs the crested wheatgrass site under season-long exposure to grazing; and (3) native prairie sites under twice-over rotational grazing vs native prairie sites under season-long grazing. The first comparison determined whether crested wheatgrass and native prairie habitats supported similar grasshopper population parameters. The second comparison assessed the effects of relatively heavy utilization by livestock early in the season at crested wheatgrass rotational sites (before turn-out on native prairie rotational sites) vs low to moderate utilization by livestock mostly later in the season at crested wheatgrass season-long sites (due to preference for native forage adjacent to the crested wheatgrass season-long site). The third comparison evaluated effects of a grazing strategy that rotated 8 distinct grazing periods over a series of 4 pastures in a different order each year vs traditional season-long grazing within a single pasture. The third comparison fulfilled the primary goal of this study.

In addition to the routine orthogonal analyses, graphs of all grasshopper life history or population parameters were examined for obvious departures from normal assumptions for the analysis of variance. Problems detected included unequal variances as well as treatment by season interactions. In such cases, the orthogonal analysis was considered misleading, and an appropriate alternative was developed and elaborated.

Results and Discussion

The Study Area

Temperature and precipitation trends during the course of this study, based on weather records from Watford City, N.D., reported by the North Dakota Agricultural Weather Network (<http://www.ext.nodak.edu/weather/ndawn>), are illustrated in Figure 1. This study obviously was conducted during an interval of progressively warmer and dryer seasons. If the hypothesis of higher grasshopper densities in the presence of low precipitation and low forage production is true, then one would expect grasshopper populations to generally increase from 1993 to 1998 at all study sites.

The 1994 and 1998 weather data from within grazing exclosures revealed no significant differences among soil degree-days between sample sites during either year, or among air degree-days between sample sites during 1994. In 1998, air degree-days at the warmest site differed significantly ($P = 0.051$) from the coolest site, but neither differed from any other site based on Duncan's multiple range test. The extreme sites were the 2 native prairie season-long sites, so that confirmed their credibility as a standard of comparison for possible effects of twice-over grazing. In other words, all sites had similar thermal potential to support grasshopper development, and there was no evidence of bias in site selection, at least with regard to factors like slope or aspect, which are known to influence soil and air temperatures. It should be emphasized that temperature data were obtained within grazing exclosures; therefore, there should be no major differences between grasshopper developmental parameters in comparable habitats (i.e., between crested wheatgrass sites or between native prairie sites) either in the absence of grazing or under identical grazing. If differences are then observed among grasshopper life processes that are driven primarily by tem-

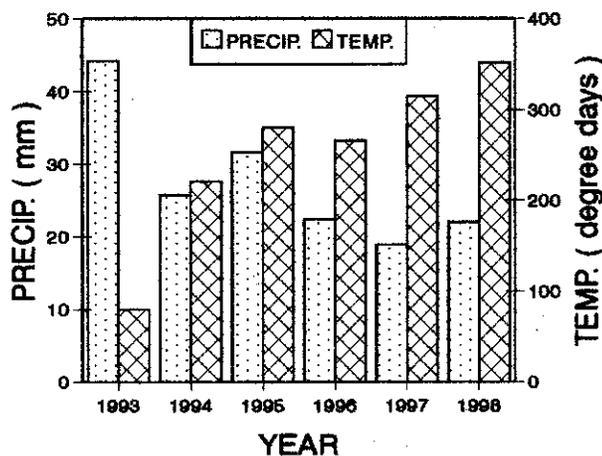


Fig. 1. Relationships between cumulative precipitation (mm) and cumulative temperature (degree-days > 17.8 C) at Watford City, N.D., 1 Apr. through 31 Sept. 1993–1998, as reported by the North Dakota Agricultural Weather Network.

perature, it should be safe to assume that the grazing regimes differentially affected grasshopper microhabitat.

A summary of 1993 and 1994 cover and biomass estimates at the study sites published by Manske (1993, 1994b, 1994c) is given in Table 1. All study sites had similar percent basal cover in 1993, but crested wheatgrass sites had less basal cover than native prairie sites in 1994. Slightly more bare ground was associated with season-long grazing than with rotational grazing at crested wheatgrass sites during both 1993 and 1994 and at native prairie sites in 1993 only. At crested wheatgrass sites, biomass was highest under season-long grazing because livestock tended to avoid eating crested wheatgrass when they had other alternatives. At native prairie sites, biomass tended to be slightly higher under rotational grazing, but stocking rates appeared to be conservative at all study sites, at least during the relatively cool and productive seasons of 1993 and 1994. In general, crested wheatgrass sites might be

expected to support higher grasshopper densities than native prairie sites, because of more bare soil at crested wheatgrass season-long sites and less total canopy at crested wheatgrass rotational sites. However, site attributes in 1993 and 1994 did not suggest that any native prairie study site would be unusually prone to chronic or abnormal infestations of grasshoppers.

Grasshopper Density Indexes

Preliminary analyses of grasshopper density and phenology data indicated that marked changes in grasshopper days (GD) from season to season were multiplicative rather than additive. Therefore, all GD values were transformed to $\ln(X+1)$ prior to final analysis. Retransformed grand means and significant P-values for all orthogonal comparisons are given in Table 2, and selected retransformed seasonal means within the different grazing treatments are illustrated in Figure 2 and Figure 3.

Table 1. Percent basal cover, percent of soil surface not covered by vegetative canopy, and total above-ground plant biomass at grasshopper sampling sites on native prairie (NP) and crested wheatgrass (CW) habitats under twice-over rotational (R) vs season-long (S) grazing in the Little Missouri National Grasslands, McKenzie County, N.D., 1993 and 1994.¹

Habitat type	Grazing strategy	Grazing season	Basal cover ²		Bare ground ³		Biomass ⁴	
			1993	1994	1993	1994	1993	1994
			(%)		(%)		(kg ha ⁻¹)	
CW	R	1 May — 31 May	39.8	24.1	3.3–10.7	2.6–3.9	823–1187	445–549
NP	R	1 Jun — 15 Oct	41.6	33.2	3.9–6.5	3.5–4.8	1004–1595	980–1504
NP	S	1 May — 15 Sep	36.2	34.5	6.0–14.1	3.6–5.5	564–1225	839–1990
CW	S	1 May — 15 Sep	36.0	26.1	0.9–17.3	6.0–10.5	1267–1491	791–1363

¹a condensation of data reported by Manske (1993, 1994b, 1994c); see references for details

²estimated mid-July to mid-Aug

³range of 4 readings, mid-May to mid-Aug

⁴range of 3 or 4 reading, late May to mid-Oct

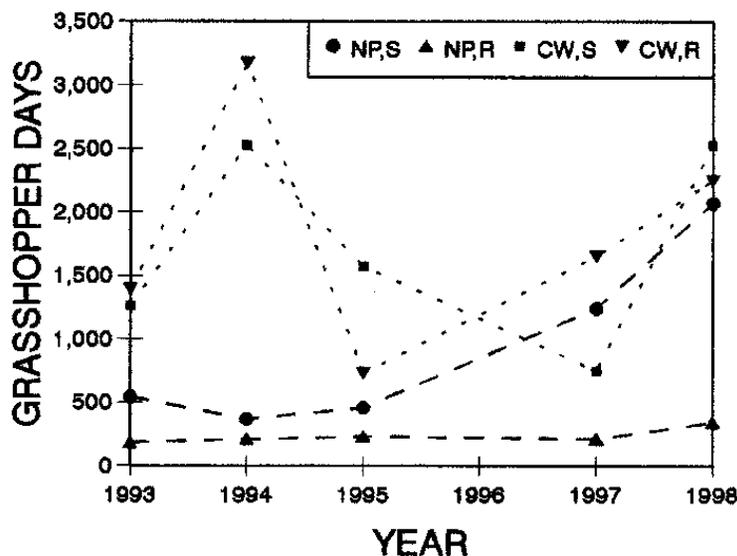


Fig. 2. Average cumulative grasshopper days (3rd instar through adult stages) m⁻² for all grasshopper species combined during each of 5 growing seasons in native prairie (NP) and crested wheatgrass (CW) habitats under traditional season-long grazing (S; dotted lines) vs twice-over rotational grazing (R; broken lines), 1993–1998.

The average grasshopper days (GD) for all grasshoppers 3rd instar or larger encountered per site per grazing treatment per season is illustrated in Figure 2. Over the course of the study, the combined crested wheatgrass sites had significantly (4.8X) more GD than the combined native prairie sites, and the native prairie season-long sites had significantly (3.3X) more GD than the native prairie rotational sites (Table 2). It is noteworthy that the dramatic increases in GD that occurred in 1997 and 1998 at all crested wheatgrass sites and at native prairie season-long sites did not occur at native prairie rotational sites; that is, the local outbreaks did not occur under the twice-over system of rotational grazing.

These results encouraged further scrutiny of the grasshopper day (GD) data for evidence of beneficial or antagonistic effects of grazing treatments upon individual grasshopper species. Although more than 30 different grasshopper species were encountered over the course of the entire study, preliminary examinations of GD data for individual species revealed that 9 of them comprised the preponderance of infestations and thus may have contributed significantly to major differences between habitats and grazing strategies. The GD data for those species were subjected to individual analyses of variance. Again, grand treatment means for each species are given in Table 2. Seasonal means for species that contributed conspicuously to local outbreaks at native prairie season-long sites are illustrated in Figure 3. The species are ranked in Table 2 according to

the order in which they normally appear during the course of a growing season (Cushing et al. 1995).

In comparisons of grasshopper days in crested wheatgrass vs native prairie sites (Comparison 1 of Table 2), 6 species were responsible for most of the higher long-term level of infestation at crested wheatgrass sites. The conspicuous spike observed for all species in 1994 (Fig. 2) was contributed primarily by single-season increases in the 2 most prevalent species, *Melanoplus infantilis* Scudder and *M. sanguinipes*. The latter, plus *A. deorum* in early spring pasture and *Phoetaliotes nebrascensis* (Thomas) in season-long pasture, accounted for most of the increased grasshopper presence on crested

wheatgrass during the last 2 years of the study. *A. deorum*, as mentioned earlier, requires patches of bare soil for basking and for oviposition. It appears that none of the native prairie sites had enough bare ground (see Table 1) to support high populations of *A. deorum*.

The comparisons of grasshopper days within crested wheatgrass habitats (Comparison 2 of Table 2) essentially addressed the question of how individual species responded to differences in timing and intensity of defoliation. It was noted that 3 of the species that preferred crested wheatgrass over native prairie, *M. sanguinipes*, *M. infantilis*, and *Melanoplus gladstoni* Scudder, seemed to thrive equally well under early spring grazing or season-long grazing. Three other species, *A. deorum*, *Trachyrhachys kiowa* (Thomas), and *Melanoplus femurrubrum* (DeGeer), developed significantly higher densities under early spring grazing, while one, *P. nebrascensis*, did just the opposite. *A. deorum* may have been prevented by high shading canopy from taking advantage of an abundance of bare soil at the crested wheatgrass season-long site (see Table 1), but otherwise, there was little evidence of a general influence of either canopy height or timing of defoliation within crested wheatgrass habitats. Rather, it appeared that grasshopper species somehow adjusted differentially to provide a similar overall density in crested wheatgrass habitats under either grazing regime.

In comparisons of grasshopper days within native prairie habitats (Comparison 3 of Table 2), no species was significantly more abundant at rotational sites than at season-long sites. However, 4 species were significantly more abundant at season-long sites than at rotational sites. In

Table 2. Mean cumulative grasshopper days per m² during 5 growing seasons under twice-over rotational (R) grazing vs traditional season-long (S) grazing at native prairie (NP) and crested wheatgrass (CW) study sites, 1993–1998; and results of orthogonal statistical tests for significant differences between means.

Species ¹	Comparison 1		Comparison 2		Comparison 3	
	All	All	CW,R	CW,S	NP,R	NP,S
	CW	NP				
All species	1619**	340	1645	1569	229	748*
<i>A. deorum</i>	31**	2	88**	4	2	2
<i>M. infantilis</i>	256**	9	258	253	5	26*
<i>M. sanguinipes</i>	455**	81	415	547	78	87
<i>T. kiowa</i>	51**	4	98**	14	3	6
<i>M. femurrubrum</i>	14	7	35**	2	9	5
<i>O. obscura</i>	4	14**	6	2	6	71**
<i>M. gladstoni</i>	53*	10	53	52	3	88**
<i>P. nebrascensis</i>	32**	8	16	126**	6	16
<i>E. costalis</i>	10	18	9	11	10	57*

¹Individual species are ranked according to order in which they appear during the season.

*Indicated mean is significantly greater than its complement P<0.05.

**Indicated mean is significantly greater than its complement P<0.01.

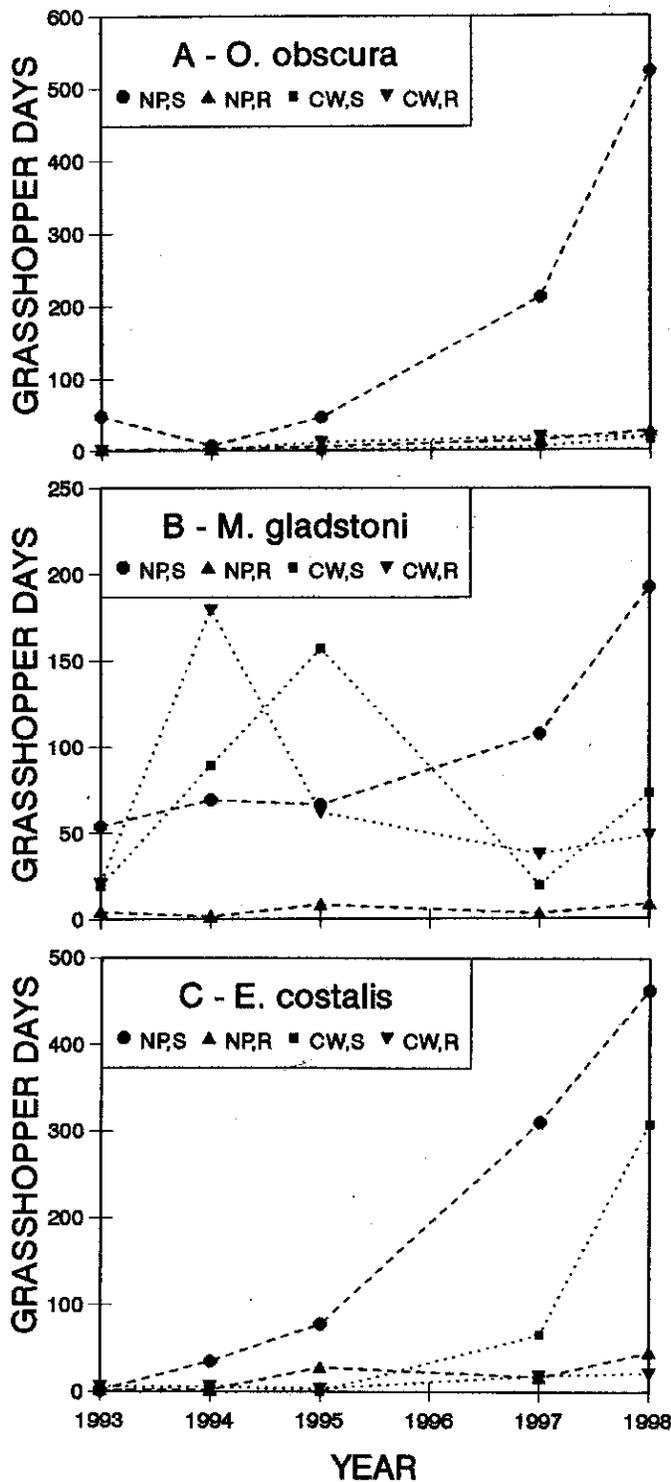


Fig. 3. Average cumulative grasshopper days (3^{rd} instar through adult stages) m^{-2} for 3 species that were highly responsive to grazing management during 5 growing seasons in native prairie (NP) and crested wheatgrass (CW) habitats under traditional season-long grazing (S; dotted lines) vs twice-over rotational grazing (R; broken lines), 1993–1998.

the case of *M. infantilis*, all populations remained relatively low and were of little or no economic concern for the duration of the study. In contrast, 3 late-season

species, *Opeia obscura* (Thomas), *M. gladstoni*, and *Encoptolophus costalis* Scudder, all increased dramatically at season-long sites during the hottest and driest

years of the study, 1997 and 1998 (Fig. 3). All 3 were major contributors to the local outbreaks at season-long sites shown in Figure 2.

O. obscura is a major pest species in shortgrass prairie, where its diet is 85 to 100% comprised of blue grama grass (Pfadt 1994). In the season-long study pasture, *O. obscura* was common either where blue grama was the primary grass species or where an understory of blue grama was exposed for much of the growing season through removal of taller, cool-season grass canopy by grazing livestock. *M. gladstoni* is a polyphagous feeder that prefers forbs but tends to ingest plants in proportion to their abundance (Mulkern et al. 1962). In the season-long study pasture, it was most abundant in associations of 2 common food sources, blue grama grass and fringed sage (*Artemisia frigida* Willd.). *E. costalis* has been described as an omnivorous granivore (Mulkern et al. 1969) that occurs "in association with heavily grazed homogeneous grass areas" (Mulkern et al. 1964). 'It is not a major pest species on all rangeland (Dysart 1995), so its biology has not been studied intensively. In the season-long study pasture, it was the last species to complete nymphal development. During late summer and early autumn, nymphs were frequently observed to take shelter for the night in cracks in the soil.

The recurring theme of late development and adaptive behavior within a sparse canopy suggests that at least some grasshopper species typically participate in a race against weather in the northern Great Plains. This provides 2 plausible explanations for the relative scarcity of late-season species under twice-over rotational grazing. First, the blue grama understory is exposed for only relatively short intervals during and immediately after the 2 grazing events. That in itself may deter species that prefer or require short canopy and intense sunlight for thermoregulation (Willott and Hassall 1998). Second, if development of late-season species is significantly delayed (as occurs regularly with *M. sanguinipes* at rotational sites), the consequences to survival could be severe. If development is extended into periods of cool nights and only short mid-day intervals of temperatures above the developmental threshold, reproduction may become impossible.

Grasshopper Density and Forage Consumption

While grasshopper day values provide

an accurate index of relative grasshopper presence, their relevance may be obscure until they are converted to more familiar units. A grasshopper day value can be converted to average density if average life span is known, and can be converted to forage consumption if a daily utilization rate is known. Such conversions are offered in Table 3 as a convenience to readers who may want to assess the practical value of observed differences between grazing strategies. Table 3 estimated density by assuming an average life span of 30 days per adult grasshopper, and estimated forage consumption by assigning average daily feeding rates reported by Hewitt and Onsager (1982) for small and medium-sized species of grasshoppers to the average grasshopper day values observed for 4th and 5th instar nymphs plus adults in this experiment. Because longevity tends to be inversely related to density (Onsager et al. 1981), the lowest densities in Table 3 probably were overestimated and the highest densities probably were underestimated. Nevertheless, an infestation as estimated at season-long sites in 1998 would be considered of outbreak proportion on any rangeland in western North America.

The estimates of forage consumption in Table 3 are considered about as accurate as allowed by current technology. If an AUM is defined as 364 kg of forage, it is noteworthy that estimated forage consumption by grasshoppers at native prairie season-long sites in 1997 reached 91% of the 0.862 AUM ha⁻¹ that had been allocated for livestock. In 1998, in spite of the 10% reduction in stocking rate, forage consumption by grasshoppers at native prairie season-long sites reached 168% of the level allocated for livestock. In contrast, maximum consumption by grasshoppers at native prairie rotational sites was 26% of the livestock allocation in 1998.

Grasshopper Life History Parameters

Only 1 species, *M. sanguinipes*, was recorded on a regular basis at every site during every year of the study. Therefore, only *M. sanguinipes* provided sufficient data to support estimation of life history parameters within all 4 grazing treatments. Nevertheless, the parameters for *M. sanguinipes* can provide important clues as to possible effects of grazing on other species as well. *M. sanguinipes* is the most serious grasshopper pest on rangeland in the United States (Dysart 1995). It occurs throughout most of North America and can develop economical infestations on

Table 3. Estimated density of grasshoppers and estimated forage consumed by 4th and 5th instar nymphs plus adults at native prairie sites under season-long vs rotational grazing in the Little Missouri National Grasslands, McKenzie County, N.D., 1993–1998.

Parameter	Grazing strategy	1993	1994	1995	1997	1998
Density (Adults m ⁻²)	rotational	2.6	1.4	3.3	2.1	5.6
	season-long	8.3	4.6	6.2	18.4	26.8
Consumption (Kg ha ⁻¹)	rotational	37.0	21.9	55.8	32.6	73.6
	season-long	124.6	59.5	97.0	287.5	474.5

range, pasture, and a variety of cultivated crops (Parker 1952). It consumes and apparently thrives on a wide array of both grasses and forbs (Mulhern 1967). It can have 2 generations per year in southern deserts and requires 2 years per generation in Alaska (Fisher 1994). In short, it can function more efficiently in more habitats than many other important economic species. Therefore, information on what is needed by *M. sanguinipes* in a given habitat may infer what is lacking for species that do not prosper there.

Certain anomalies in field data can preclude estimation of life history parameters (Onsager and Hewitt 1982a). For example, an occasional problem in this study was lower representation in a given instar than in a subsequent instar. Therefore, the number and type of parameters determined for individual sites were not constant. Interpretation of data also was complicated by a period of cold, wet weather from 29 June through 7 July of 1997, which interrupted the hatching of *M. sanguinipes* at 7 of the 9 study sites for an interval of 7 to 9 days. An advantage was that 2 distinct waves of hatchlings permitted estimation of 2 unique sets of nymphal developmental parameters at some sites within a single season. The disadvantage was that nearly all nymphs at the earliest site (a crested wheatgrass rotational site) hatched before the cold spell while all of the nymphs at the latest site (the crested wheatgrass season-long site) hatched after the cold spell.

Consequently, slow development and low survival of nymphs at the former site in contrast with fast development and normal survival of nymphs at the latter site affected experimental errors and increased the probability of a Type I error in any comparison that included a crested wheatgrass treatment. Therefore, only comparisons between native prairie treatments (i.e., comparison #3 of the orthogonal set) were considered statistically valid. These are given in Table 4.

The Julian day associated with peak presence of various life stages is a useful index of grasshopper phenology (Kemp and Onsager 1986). The phenology of *M. sanguinipes* at 4th peak instar was essentially identical for the 2 native prairie treatments (Table 4), and that conclusion was worthy of special emphasis. When subsequent parameters were found to differ significantly between native prairie sites, lack of phenological synchrony could be dismissed as a plausible cause. Equivalent development tended to occur earlier on the crested wheatgrass rotational sites, presumably because intensive forage removal began there about 4 weeks earlier and the grasshopper microhabitat warmed up faster than at any of the other sites. Equivalent development occurred later at the crested wheatgrass season-long site, presumably because livestock tended to avoid grazing crested wheatgrass out of preference for native forage.

Table 4. Life history parameters for *Melanoplus sanguinipes* as affected by twice-over rotational grazing vs traditional season-long grazing of native prairie in the Little Missouri National Grasslands, McKenzie County, N.D., 1993 to 1998.

Parameter	N ¹	Grazing strategy		P
		Rotational	Season-long	
Julian day for peak presence of 4 th instar nymphs	6	204.3	204.1	0.89
Stage-specific survival rate for nymphal instars 3–5				
Mean	20,11 ²	0.512	0.662	0.06
Variance		0.027	0.073	0.03
Days for development per instar	6	11.5	8.9	0.02
Average daily survival rate for nymphal instars 3–5	6	0.94238	0.95418	0.53
Adults produced per square meter	4	0.60	2.05	0.03
Average daily survival rate for adults	5	0.99346 ³	0.97345	0.02

¹number of broods for which parameter was estimated at least once per grazing strategy.

²total number of study sites at which parameter was estimated within rotational and season-long strategies, respectively (see text for justification)

³aberrant (see text for explanation).

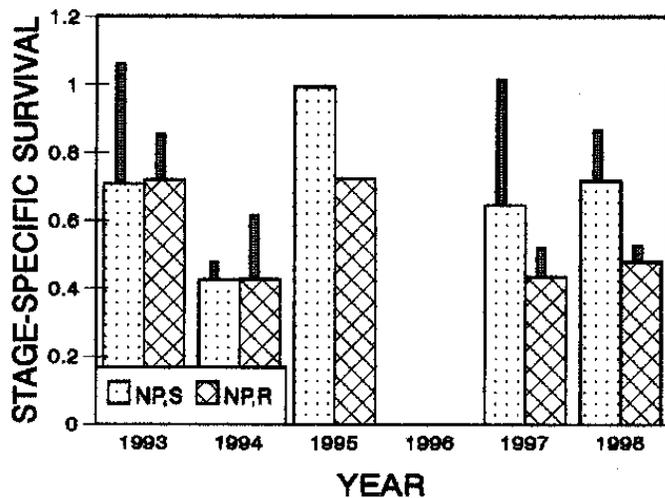


Fig. 4. Mean stage-specific survival rates for 3rd, 4th, and 5th instar nymphs of *M. sanguinipes* during 5 growing seasons between 1993 and 1998 on native prairie (NP), as affected by traditional season-long grazing (NP,S) vs twice-over rotational grazing (NP,R) (error bars indicate standard deviations).

Average stage-specific survival rates for 3rd, 4th and 5th instar nymphs of *M. sanguinipes* at native prairie study sites are given in Table 4 and Figure 4. The routine orthogonal analysis indicated no difference between treatment means, but Figure 4 revealed a treatment by year interaction plus significantly greater variance within season-long sites than within rotational sites. The data were reanalyzed as a completely random design comprised of 2 treatments with unequal variances, and a P-value of 0.06 was obtained. That was considered justification to report lower and more stable stage-specific survival rates under rotational grazing than under season-long grazing. The observed individual stage-specific survival rates as well as the overall average rates were considered entirely realistic. They compare favorably with rates of 0.3993 to 0.8087 reported for natural populations of *M. sanguinipes* during different seasons at the same site near Roundup, Mont. (Onsager and Hewitt 1982a) and at different sites during the same season near Three Forks, Mont. (Sanchez and Onsager 1988). Stage-specific survival rates of 0.09 to 0.365 were reported for nymphs of 3 species, one of which was *M. sanguinipes*, in cage studies in the sand hills of Nebraska (Oedekoven and Joern 1998).

A stage-specific survival rate can be partitioned mathematically into an average daily survival rate (S) and days (d) required for development of a stage. Thus, stage-specific survival was defined to be

(S^d), and $S = (S^d)^{1/d}$. If any 2 parameters are known, the third can be calculated. There obviously is an infinite set of values for d and S that will yield an identical stage-specific survival rate, so each observed stage-specific survival rate was partitioned to determine the range of d- and S-values that occurred within each grazing treatment during the experiment.

Nymphs at all crested wheatgrass sites tended to develop either slightly faster (i.e., d was slightly lower) than or at rates similar to development of nymphs at

native prairie season-long sites. At native prairie rotational sites, nymphs developed significantly slower than at native prairie season-long sites (Table 4). The average difference between treatment means (i.e., 2.6 days per instar), extended over 3 instars, would delay the appearance of adults under rotational grazing by an average of 7.8 days. That will be shown later to have a major impact on the proportion of nymphs that became adults. The averages, however, did not depict the full relationship observed in this study. While d was relatively constant from year to year at the native prairie season-long sites, it decreased (i.e., the rate of development increased) significantly over the experimental period at the native prairie rotational sites (Fig. 5). During the coolest year of the study (1993), nymphs at native prairie rotational sites required about 14 days per instar, which was about 5.1 days longer per instar than at native prairie season-long sites. Logical hypotheses to explain these results are that ambient air temperatures within the canopy were cooler at native prairie rotational sites, or that nymphs were somehow deprived of opportunity for efficient thermoregulation at native prairie rotation sites [see Chappell and Whitman (1990) for a discussion of thermoregulation]. Either condition could have produced the observed results, either independently or in combination with the other. During the warmest years of the study (1997 and 1998), d was similar at all native prairie sites. A plausible explana-

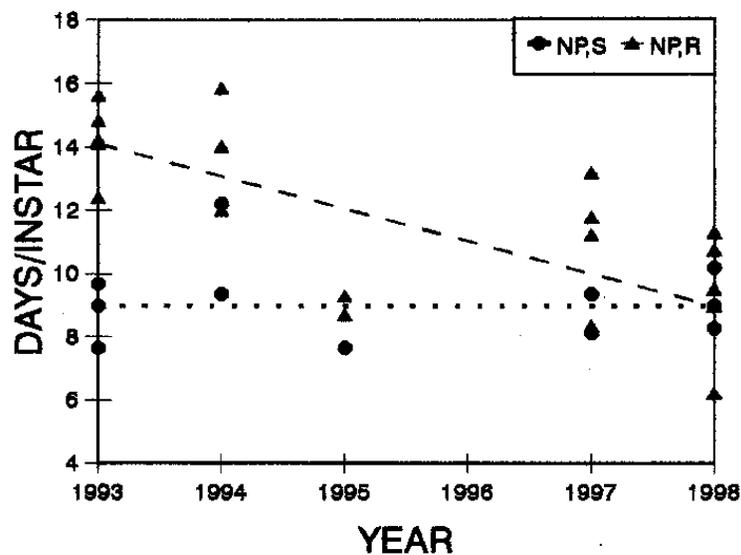


Fig. 5. Average number of days required by *Melanoplus sanguinipes* for development of 3rd, 4th, or 5th instar stages during 5 growing seasons between 1993 and 1998 on native prairie (NP), as affected by traditional season-long grazing (NP,S; dotted line) vs twice-over rotational grazing (NP,R; broken line).

tion is that nymphs at native prairie season-long sites may have invested considerable time in avoiding excessive body temperatures, the result of exceeding a thermal optimum, during the warmer later years, and therefore did not develop significantly faster than during the cooler earlier years.

While the average daily survival rate for nymphs (S_n) tended to be slightly higher at crested wheatgrass sites than at native prairie sites, the tests for statistical significance were not considered reliable. In legitimate comparisons, S_n did not differ significantly between grazing strategies at native prairie sites. However, a difference of the magnitude observed in Table 4 (i.e., a difference of 0.01180) can have major consequences if it operates over sufficient time. For example, when Sanchez and Onsager (1994) arbitrarily reduced estimated average daily survival rates of adults (S_a) by 0.00428 and 0.00786 to adjust for the presence of parasitized females that were unable to produce eggs, the predicted rates of population increase were reduced by about 32% and 51%, respectively, and they then agreed closely with observed rates. It also is critical to understand that an average daily mortality rate (i.e., $1 - S_n$) would continue unabated during any period of extended development at native prairie rotational sites. If we assume that "normal" development requires 8.9 days for each of 3 instars as observed at native prairie season-long sites, then the fraction of 3rd-instar nymphs that survived to become adults at native prairie rotational sites can be estimated for 1993 as $100(0.94238^{3(14-8.9)}) = 40.3\%$ of "normal", for the 5-year average of the study as $100(0.94238^{3(11.5-8.9)}) = 62.9\%$ of "normal", but for 1998 as $100(0.94238^{3(8.9-8.9)}) = 100\%$ of "normal".

Figure 6 illustrates some interesting and diametrical relationships between days per instar and survival rate (i.e., between d and S_n) at native prairie sites. Two of the data points in Figure 6 clearly were atypical. The 2 lowest S_n -values were excluded from this discussion because they are indicative of catastrophic conditions, they occurred among nymphs that had hatched before the cold, wet period in late June and early July of 1997, and they probably were induced by a local epizootic of pathogenic fungi as has been reported in other infestations (Onsager and Hewitt 1982a). Among the remaining data points in Figure 6, there was significant inverse correlation ($r = -0.75$, $P = 0.038$) between d and S_n at native prairie season-long sites and significant direct correlation ($r = 0.83$,

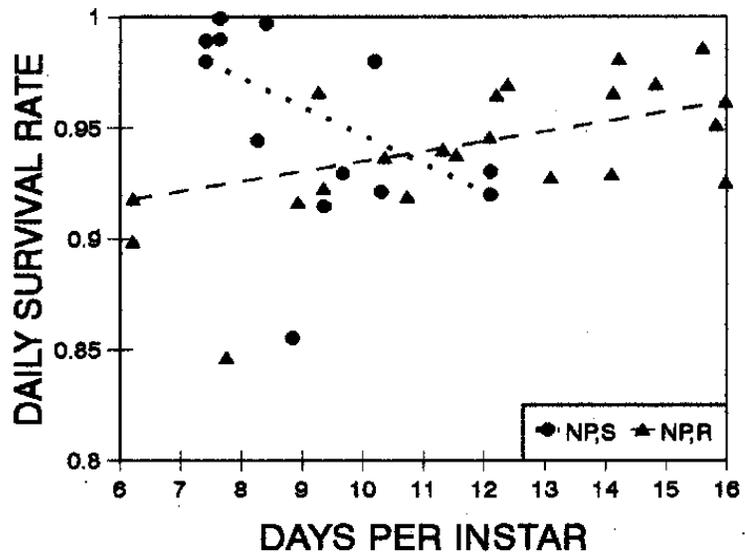


Fig. 6. Relationships between average daily survival rates vs average number of days required by *Melanoplus sanguinipes* for development of 3rd, 4th, or 5th instar stages during 5 growing seasons on native prairie (NP), as affected by traditional season-long grazing (NP,S; dotted line) vs twice-over rotational grazing (NP,R; broken line) strategies.

$P = 0.012$) at native prairie rotational sites. This paradox cannot be explained with the data at hand, but speculation clearly labeled as such is offered. Grant et al. (1993) suggested that S_n may well be lower during seasons characterized by high rainfall and low sunshine, rather than by low temperature per se, because nymphs will be less active and more liable to predation. The current data obviously do not support that hypothesis. Figure 6 may be evidence of a bimodal response of daily survival rates to the heat-related factors that drive nymphal development. At the cooler extremes, conditions that extend nymphal development of *M. sanguinipes* to 15–16 days per instar perhaps could inhibit activity or development of invertebrate predators that are inherently less adaptable than *M. sanguinipes*. At the warmer extremes, conditions that allow *M. sanguinipes* to complete a nymphal instar in only 7–8 days could perhaps allow nymphs to escape some predation by developing ahead of invertebrate predators to which they normally would be vulnerable. In any event, it is apparent in Figure 6 that all intermediate development times (i.e., on the order of 9–12 days per instar) were associated with similar nymphal survival rates, regardless of grazing treatment. Therefore, a worthwhile management objective would be to retain canopy characteristics that extend development to 13–16 days per instar. Even though the associated daily survival rates may be slightly higher than lowest possible rates,

the extra time over which the higher rates operate will yield the lowest possible overall level of nymphal survival. The relative importance of the 2 parameters in this study is therefore under some conditions reversed from the order reported by Grant et al. (1993).

The mean estimated density of adult *M. sanguinipes* produced at native prairie rotational sites was significantly lower than (i.e., was only 29% of) the number produced at native prairie season-long sites (Table 4). Using the average nymphal parameters of Table 4, the model of Onsager (1983) estimated that the 2 average infestation levels could have risen from similar average densities of hatchlings (about 18.2 vs 16.5 hatchlings m^{-2} , respectively). This is a classic example of the powerful impact that can be induced by forcing slightly reduced survival rates to function over slightly extended intervals of time.

The average daily survival rate for adults (S_a) differed significantly between grazing treatments (Table 4). The current average S_a for native prairie season-long sites was markedly higher than in a study on mixedgrass prairie when *M. sanguinipes* populations declined for 3 successive seasons (Onsager and Hewitt 1982b). It was only slightly higher than in a 1-year study on crested wheatgrass where 2 populations almost replaced themselves (Sanchez and Onsager 1988). In Onsager's (1983) model, it was suggestive of a generation that is capable of

approximately doubling in density. Therefore, the 5-year average S_a for native prairie season-long sites in this study was entirely realistic. However, a 5-year average S_a in excess of 0.99, as reported for the native prairie rotational sites, is unprecedented and therefore considered biologically untenable. That value indicates the consistent presence of more adults than can be accounted for by presence of nymphs, and is clear evidence of consistent immigration of adult *M. sanguinipes* into the native prairie rotational sites. Unfortunately, it is not possible to recapture either true values for S_a or precise levels of immigration. However, if the observed densities of resident adults did indeed develop from similar densities of hatchlings, then immigrant adult females must have outnumbered resident adult females by about a 2.4:1 ratio at native prairie rotational sites in order to produce the required total number of eggs. At this point, lest someone question the wisdom of a grazing system that encourages immigration of grasshoppers, it should be pointed out that grasshoppers will leave areas with poor food resources and invade areas with good food resources. Therefore, if there is a choice, a ranch should strive to become a refuge for rather than a source of migrating grasshoppers.

Conclusions

These results agree with the earlier reports that associated high grasshopper populations with hot, dry weather in the Great Plains. They strongly suggest that grasshoppers could be responding primarily to levels of available heat (see Willott and Hassall 1998), which are affected by relationships between moisture levels and plant canopy density and which are modified by thermoregulatory behavior (see Willott 1997). That notion supports interesting speculation about future infestations at the study sites. Infestations in all crested wheatgrass habitats will likely remain high and variable regardless of future weather conditions or grazing strategy, with the species complex, especially *M. sanguinipes* and *M. infantilis*, adjusting to take advantage of forage resources that are not utilized by livestock. If current drought intensity continues or increases, it is expected that permanent prime habitat for late-developing species within the native prairie season-long pasture could support total densities similar to or only slightly higher than densities observed in 1998. Under those weather conditions, however,

a further increase in intermittent acceptable habitat would probably promote rapid and dramatic increases in overall numbers of at least *E. costalis*, *O. obscura* and *M. gladstoni*. In contrast, the low populations of those species at native prairie rotational sites would require perhaps 3–4 consecutive favorable seasons in order to increase to levels comparable to 1998 at native prairie season-long sites. In the event of continued drought, *M. sanguinipes* is the only species at native prairie rotational sites that could likely increase to outbreak levels within 2 seasons.

Concepts and technologies developed for grasshopper management in the northern Great Plains probably will not transfer directly to Palouse prairie, intermountain sagebrush, or shortgrass prairie ecosystems. In an 8-year study at a Palouse prairie site in western Montana, Belovsky and Slade (1995) reported that grasshopper density, survival, and reproduction responded directly in a density-dependent fashion to natural and experimental changes in availability of food. Annual changes in food abundance were associated with the annual variation in weather (rainfall and temperature), but most grasshopper generations produced more nymphs than the habitat could support, followed by accelerated mortality until grasshopper numbers matched the food supply. That mechanism would support the close relationship between long-term mean density and long-term carrying capacity reported for western Montana by Kemp and Dennis (1993). In a study of grasshopper density data and weather records over a 27-year period in the intermountain sagebrush ecoregion of southern Idaho, Fielding and Brusven (1990) reported that abundant winter precipitation and warm spring and summer temperatures were associated with high grasshopper populations, presumably through favorable effects on forage production. Similar studies on predominantly shortgrass prairie in Colorado and New Mexico (Capinera and Horton 1989) revealed that grasshoppers responded favorably to spring and summer moisture, which also would support abundant forage production. In a study on shortgrass prairie in Arizona, Nerney and Hamilton (1969) reported increased grasshopper populations after seasons with above-average winter and spring precipitation followed by abundant vegetative cover. Furthermore, both Fielding and Brusven (1995), in the intermountain ecoregion, and Capinera and Sechrist (1982), in the shortgrass prairie ecosystem, reported higher grasshopper densities at ungrazed sites

than at grazed sites. These reports agreed that grasshopper densities were regulated by food abundance and increased to "outbreak" levels under above-average precipitation and above-average forage production. Fielding and Brusven (1996) suggested that such conditions may not cause undue competition between grasshoppers and livestock for available forage. Thus, prevention of such infestations may be unnecessary, undesirable, or impossible. (This does not deny the importance of severe infestations during normal seasons that follow unusually-productive seasons, or the importance of immigration of grasshoppers from rangeland to crops, but those problems are beyond the scope of this discussion.)

A grazing strategy that dampens fluctuation in grasshopper nymphal survival rates might also dampen fluctuation in density. According to the equilibrium parameters of Kemp and Dennis (1993), that could reduce the propensity for outbreaks in the northern Great Plains, especially if the grazing strategy tended to stabilize nymphal survival at a lower rate than otherwise expected. Twice-over rotational grazing appears to have reduced both the mean density and the carrying capacity of grasshoppers on native prairie. In general, both speculation and scientific evidence to date agree that twice-over rotational grazing has mitigated a localized grasshopper outbreak. Thus, grasshopper management through grazing management may be eminently practical in the northern Great Plains.

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Sward quality affected by different grazing pressures on dairy systems

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Abstract

The objective of the experiment was to examine the effects of different stocking densities (3.7, 4.6, and 5.5 cows ha⁻¹) on tiller density, botanical composition, and chemical (crude protein [CP], acid detergent fiber [ADF], Ca, P, K, and Mg) quality of pasture and the seasonal (before flowering [spring], after flowering [summer], and autumn) distribution of these parameters. Percentages of sown [perennial ryegrass (*Lolium perenne* L. cv 'Brigantia') and white clover (*Trifolium repens* L. cv 'Huia')] and volunteer species were not significantly affected by stocking density, although as stocking density increased, tiller density also increased. This effect was more pronounced for volunteer species than sown species. Density was significantly higher before flowering than after flowering or autumn. Stocking density affected the chemical quality of herbage with ADF, CP, P, K, and Mg higher at high stocking density. The Ca/P relationship was lower at high stocking density, but the K/(Ca+Mg) relationship was not significantly affected by stocking density. Chemical quality of the pasture was higher before flowering than after flowering or autumn. The Ca/P ratio exceeded the upper limit recommended for dairy cows, but no osteomalacia was found in the present experiment. Low values of the K/(Ca+Mg) ratio were found in the spring. Therefore, on these pasture types it is advisable to use concentrates high in Mg or Mg supplements in the spring in order to avoid hypomagnesemia.

Key Words: *Lolium*, stocking rate, *Trifolium*

Pasture production and its seasonal distribution are important variables which determine animal production. However, it is important to know other characteristics relating to the sward such as density (number of tillers per square meter) and botanical composition, which can affect pasture production and herbage intake. Density and botanical composition are usually affected by management decisions, such as stocking rate or density (Curll and Wilkins 1985, Baker and Leaver 1986).

Forage intake is dependent on the availability of forage, on the chemical and physical composition of the forage, and on the nutritional requirements of the animal (Minson 1982). Therefore,

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Resumen

El objetivo de este experimento fue evaluar el efecto de diferentes cargas ganaderas (3.7, 4.6 y 5.5 vacas ha⁻¹) sobre la densidad, composición botánica y calidad química (proteína bruta (PB), fibra ácido detergente (FAD), Ca, P, K y Mg) del pasto y la distribución estacional (antes de la floración [primavera], después de la floración [verano], y otoño) de estos parámetros. Los porcentajes de las especies sembradas [raigrás inglés (*Lolium perenne* L. var "Brigantia") y trébol (*Trifolium repens* L. var 'Huia')] y espontáneas no se vieron significativamente afectados por la carga ganadera, sin embargo a medida que la carga ganadera aumentó, la densidad del pasto se incrementó. Este efecto fue más pronunciado para las especies espontáneas que para las sembradas.

La densidad fue significativamente mayor antes de la floración que después de la floración o en otoño. La carga ganadera afectó a la calidad química de la hierba, resultando los contenidos en FAD, PB, P, K, y Mg mayores con las cargas más altas. La relación Ca/P fue menor en las cargas altas, sin embargo la relación K/(Ca+Mg) no fue significativamente afectada por este parámetro. La calidad química del pasto fue mayor antes de la floración que después de este período o en otoño. A pesar de que la relación Ca/P fue mayor que el límite superior recomendado para vacas de leche, no se encontraron casos de osteomalacia en este experimento. Se encontraron valores bajos de la relación K/(Ca+Mg) en la primavera. Por lo tanto en este tipo de pastos es recomendable utilizar concentrados ricos en Mg o complementados con Mg en primavera para evitar problemas de hipomagnesemia.

herbage quality is an important factor which affects animal production, and knowledge about its seasonal distribution is necessary to make management decisions such as use of supplements or calving dates.

Chemical analysis of pasture is an indirect method of determining availability of an element to an animal. It is important to know the mineral contents of pastures which are grazed because there are some important differences with ungrazed pastures (Frame and Hunt 1971). Mineral content, that exceeds or falls short of the optimal requirements of grazing animals can cause health and production problems. Milk fever or hypocalcaemia (Pickard 1986, Grace 1983a, Minson 1990) is a pathology related to a deficit of calcium in dairy diet and can lead to occasional bone disorders. Hypomagnesaemia or grass tetany is produced when magnesium is not given in adequate proportion in the diet and causes mainly a reduction on milk production and fertility of

cows (Pickard 1986, Minson 1990, Grace 1983a). Deficiency of potassium is not usual as pasture has substantial percentage of this element, but if it is in excess then it will cause problems with magnesium absorption and therefore precipitate hypomagnesaemia (Minson 1990).

Protein content and ADF of pasture are related to intake (Mott 1983, Minson 1982) and are affected by climatic conditions (Munro and Walters 1985, Metson and Saunders 1978b, Roberts 1987, Stehr and Kirchgessner, 1976).

Our objective was to determine the effect of differing stocking densities on botanical composition, density, and chemical characteristics (ADF, CP, and mineral content) of dairy system pastures in Spain, as well as the seasonal distribution of these parameters.

Materials and Methods

The experiment was carried out in Mabegondo (Galicia region)(43°15' N, 8°18'W) during 3 years of a dairy systems study. In the study, 3 treatments were established: Treatment A was pasture only and Treatment B was a pasture plus corn+rye (*Zea mays* L.+ *Secale cereale* L.) for silage. Both Treatments A and B had an overall stocking rate of 2.5 cows ha⁻¹. Treatment C was also a pasture plus corn+rye silage system, but the overall stocking rate was 3 cows ha⁻¹. Due to the different overall stocking rates and land area allocated for grazing vs. corn+rye or forage-based silage production, the effective stocking densities for the pasture component of each treatment differed during the year and are shown in Table 1. The average stocking density for the grazing component of the treatments was 3.7, 4.6, and 5.5 cows ha⁻¹ for A, B, and C, respec-

Table 1. Stocking rates (cow ha⁻¹) for each treatment and period pre-flowering (pre), post flowering (post) and autumn for 1989, 1990, and 1991.

		Treatment		
		A	B	C
		----- (cows ha ⁻¹) -----		
1989	pre	4.93	5.00	5.55
	post	4.32	4.58	5.74
	autumn	2.47	4.17	5.65
1990	pre	4.93	5.00	5.55
	post	2.87	4.56	5.72
	autumn	2.73	4.72	5.65
1991	pre	4.93	5.00	5.55
	post	2.78	3.92	5.09
	autumn	3.57	4.69	5.47

tively. The effect of the 3 stocking rates on animal production and on pasture production had been evaluated by Mosquera and González (1998, 1999).

The total area for the systems studied was 8.1, 8.0, and 6.7 ha for treatments A, B, and C, respectively. Each treatment was grazed with Friesian breed dairy cows with live weights of approximately 500 kg.

For all treatments, the pasture area was sown with a mixture of 22 kg ha⁻¹ perennial ryegrass cv. Brigantia and 4 kg ha⁻¹ white clover cv. Huia. On average, the swards were 5 years old and they contained about 60% sown species (mostly perennial ryegrass) at the start of the experiment.

Grazing management

Cows were rotationally grazed across paddocks from March until the forage supply was limited by drought. The average number of grazing days per paddock was around 1.9 and the average regrowth period was 25 days. Areas reserved for grass silage production were all cut before flowering (15 May) and then integrated into the grazing cycle if necessary in the autumn. During the summer, cows were

usually fed silage until autumn growth provided enough herbage to graze. Cows resumed grazing in the autumn after sufficient herbage mass had accumulated after the summer drought and continued grazing until herbage production was limited by cold temperatures.

While grazing, cows were offered a similar daily herbage allowance (around 15 kg cow⁻¹ day⁻¹). This was achieved by changing regrowth period and grazing days.

Measurements

In each paddock, 5 random samples of available herbage were taken just before grazing (0.33 x 0.33 m area cut to 2.5 cm above ground level). Samples were taken every time that cows were moved into a paddock in each rotation. Samples were stored at 4°C until processing (never more than 5 days). Samples were dried (70°C for 24 hours) and weighed. Acid detergent fiber was determined by the method of Goering and Van Soest (1970). A micro-Kjeldahl digestion technique, modified auto-analyzer, was used to determine simultaneously total N (%) and P (%) concentration (Castro et al., 1990). Calcium (%), K (%), and Mg (%) were determined by atomic absorption spectrophotometry by using a Perkin-Elmer 460 spectrophotometer. The relationships Ca/P (%) and K/(Ca+Mg)(meq/meq) were calculated.

To determine botanical composition, in 1990 and 1991, a 100 g subsample of fresh herbage was collected from each paddock just before grazing by cutting five, 1 m² areas to 2.5 cm above ground level. Subsamples of 100 g were taken at random and species were hand-separated, dried (70°C for 24 hours) and weighed individually for estimating composition based on dry weight. Tiller density was determined in 1991 by taking forty, 5-cm diameter cores from each grass paddock just before grazing to measure tiller population densi-

Table 2. Percentage of sown *Lolium perenne* L. and *Trifolium* sp., dead matter (dead) and volunteer species in spring (before flowering), summer (after flowering) and autumn in 1990 and 1991 in each treatment.

Species	Treatment			Sig.	Period			Sig.
	A	B	C		Spring	Summer	Autumn	
----- (%) -----								
1990:								
Sown	27.37±21.8	32.09±13.7	34.84±13.8	ns	48.85a±3.6	28.22b±9.6	17.23b±4.4	**
<i>Lolium perenne</i>	26.04±20.8	30.27±12.2	32.77±12.8	ns	46.03a±4.0	26.25b±9.0	16.81b±4.1	*
<i>Trifolium</i> sp	1.32±1.1	1.82±1.5	2.06±1.0	ns	2.82a±0.4	1.97b±0.5	0.42c±0.3	**
Volunteer	63.11±15.0	58.91±12.1	57.87±9.9	ns	49.81b±3.0	57.25a±9.7	72.83a±3.8	*
Dead Material	9.51±8.3	8.99±6.9	7.29±5.1	ns	1.33a±0.6	14.52b±3.4	9.94b±0.8	***
1991:								
Sown	23.35±8.2	27.55±2.6	30.49±3.4	ns	29.03±5.8	24.12±7.6	28.24±3.3	ns
<i>L. olium perenne</i>	19.55±5.5	25.31±3.2	26.39±5.5	ns	27.22±5.5	22.41±7.1	21.62±1.6	ns
<i>Trifolium</i> sp	3.80±3.5	2.24±0.8	4.10±2.1	bs	1.81a±0.4	2.50b±0.9	5.83b±2.4	*
Volunteer	72.18±10.2	69.87±2.4	67.07±3.0	ns	69.26±5.6	71.98±7.4	67.88±6.2	ns
Dead material	4.46±2.6	2.58±1.8	2.43±0.7	ns	1.70±0.4	3.89±0.7	3.87±2.9	ns

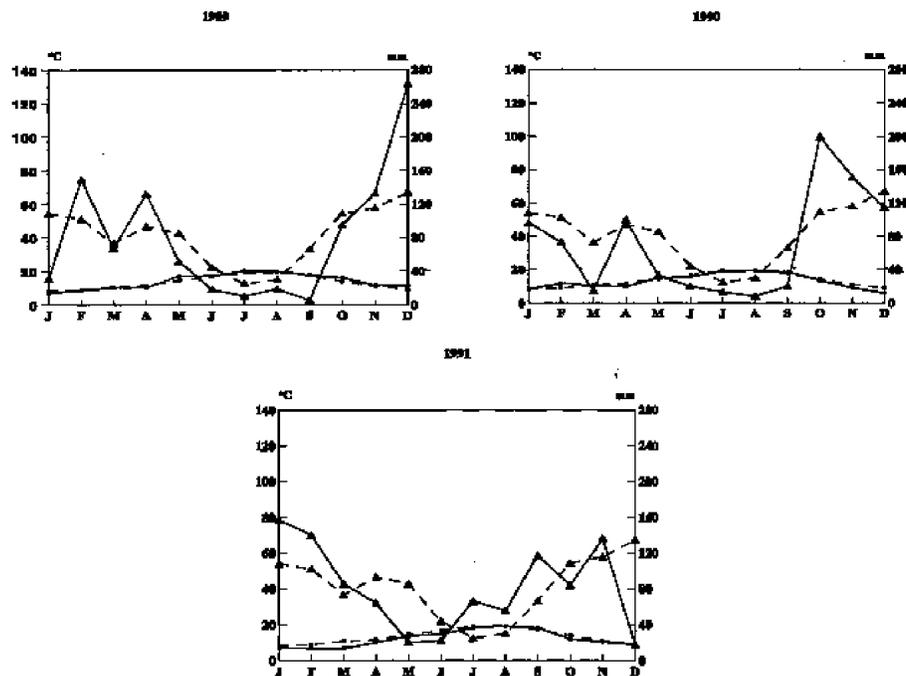


Fig. 1. Monthly rainfall (mm) and average temperatures (°C) for each studied year (continuous line) and monthly rainfall mean of the last 20 years (1978–1998) and average temperature of the last 12 years (1986–1998) (discontinuous line).

ty in each treatment. Visual estimations of dead matter and bare ground were made on each core as were tillers (every shoot and root was one tiller).

The treatment and period effect on botanical composition, tiller density, ADF, CP, and mineral content of pasture were statistically analyzed with a two-way ANOVA. Treatment was considered as random factor and period as fixed factor as described in Little and Hills (1987) and Stockdale and King (1980). Three periods were established: before and after flowering (date of flowering is considered to be on 10 May) and autumn (starting on 10

October). Means were separated by using L.S.D. test.

Results

Climatic conditions

Monthly rainfall and average temperatures for each year are presented in Figure 1. Herbage growth was usually restricted by dry conditions from July to October. In 1991, there was a dry period between May and June and an unusually wet summer (mainly July and August).

Botanical composition

Percentages of volunteer and sown species in each treatment and period are presented in Table 2. The percentages of sown and volunteer species were not significantly affected by the stocking density, but there was a tendency towards a higher percentage of sown species at the 2 higher stocking densities in 1990 and 1991.

In 1990, the percentage of volunteer species was higher in the summer and autumn than in spring, and the amount of dead material was lower in the spring. However, no differences were found for these parameters in 1991. White clover content was lower in autumn in 1990, compared to autumn 1991. In that year white clover content was higher in autumn than the other seasons. These results could be explained by the wet summer in 1991, which permitted the recovery of white clover plants along with a lesser amount of dead tissue. Perennial ryegrass was significantly lower in summer and autumn in 1990 but did not vary due to season in 1991.

Tiller density is shown in Table 3. Increased stocking density increased tiller density of the sward. Total tiller density of Treatment C was double that of Treatment A. The effect of stocking density was more pronounced for volunteer than sown species.

Of the volunteer species, *Agrostis tenuis* Sibth., *Poa pratensis* L., *Holcus lanatus* L., and *Plantago lanceolata* L. comprised about 67, 63, and 41% of total volunteer species in Treatments A, B, and C, respectively. Density of these individual species was not affected by the treatment. Increased plant density at the higher stocking density was due to the increased presence of *Bellis perennis* L. and *Geranium molle* L., which represented 30 and 12%, respectively, of the volunteer species in Treatment C. These species were present at only low numbers in the other treatments.

The density per grazing period is shown in Table 4. Densities of both volunteer and sown species were generally higher before flowering than for the other 2 periods although this varied among species.

Numbers of tillers m² of perennial ryegrass, white clover, *H. lanatus*, and *P. pratensis* were lower in autumn and summer than in spring. However, *P. lanceolata* had a higher percentage of tillers in autumn than in the summer or spring.

Species percentages obtained by weighing differed from that found by counting the number of tillers. Based on tiller numbers, the total volunteer species percentage was higher (82%) at the high stocking density (Treatment C) than in Treatments A (76%) or B (73%). However based on

Table 3. Sward density of different species in each treatment during 1991 (tillers m⁻²)

Species	Treatment			Sig.
	A	B	C	
Total	8198a±1329	13735b±7086	16974b±11677	*
Sown:				
<i>Lolium perenne</i>	1755± 441	2433±1437	2221±1159	ns
<i>Trifolium repens</i>	180± 00	1210± 300	766± 680	ns
Total	1955± 484	3643±2379	2977± 495	ns
Volunteer:				
<i>Plantago lanceolata</i>	944± 196	996± 530	1277± 785	ns
<i>Holcus lanatus</i>	2016±1602	2124±1375	2079±1452	ns
<i>Agrostis tebyus</i>	2968± 878	2989± 545	2402±1046	ns
<i>Dactylis glomerata</i>	204± 142	203± 251	153± 21	ns
<i>Bellis perennis</i>	62± 21	200± 40	4088±6851	ns
<i>Poa sp</i>	465± 388	2674±3696	1277±1404	ns
<i>Geranium molle</i>	24± 10	131b± 143	1877±3242	ns
Total	6242a± 846	10091b±4728	13997b±11500	*
Dead matter (%)	8.68 ±2.48	3.21±6.66	8.68±4.96	ns
Bare soil (%)	49 ±7.27	55 ±21.6	38 ±3.83	ns

ns: not significant; *: p<0.05

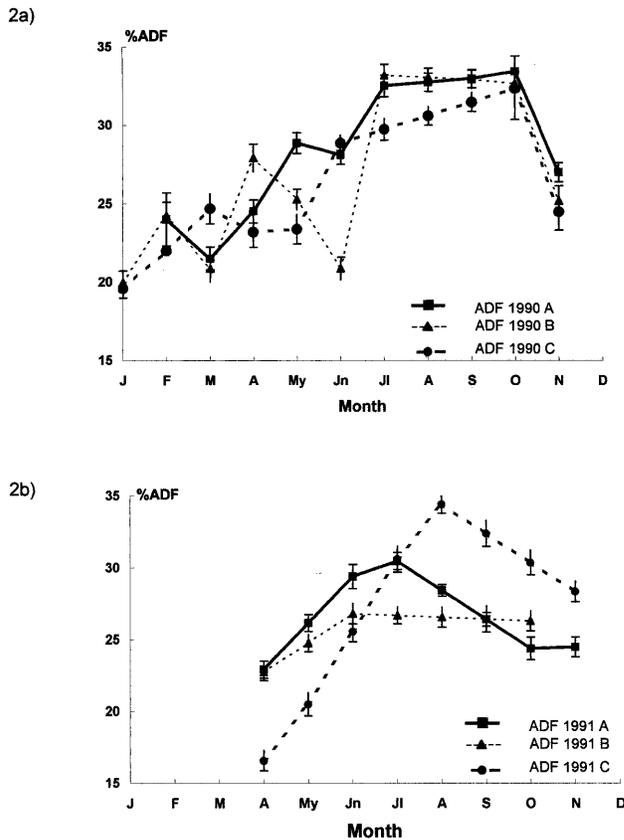


Fig. 2. Seasonal distribution of ADF for the treatments A, B, and C, in 1990 and 1991.

weight, percentage of volunteer species was lower in Treatment C (59%) than either Treatment A (73%) or B (71%). This was because, although more numerous, the prostrate growth habit of the volunteer species made very little contribution to herbage mass.

Protein, ADF, and mineral composition of pasture

Two year average for sward CP, ADF, and mineral concentration and ratios for the three stocking density treatments and pre-flowering, post-flowering, and autumn periods are shown in Table 5. Acid detergent fiber was not affected by the increase of stocking density and averaged 26%. Seasonal variation in ADF for 1990 and 1991 for each stocking density is presented in Figure 2a and 2b. Information from 1989 was omitted because it was very similar to 1990. Both years, ADF was lowest in the spring before flowering and highest in the summer.

Crude protein (Table 5) concentration was lowest at the lowest stocking density, Treatment A. But, because forage availability was 68 and 211 kg ha⁻¹ more in 1990 and 1991, respectively, on treatment A than on treatments B and C, the kilograms of protein offered to cows were sim-

ilar for all 3 treatments (244.14, 246.02, and 247.30 kg ha⁻¹ for Treatments A, B, and C, respectively). Seasonal variation in CP concentration was similar for all treatments (Fig. 3a and 3b), starting off high in the spring, declining in the summer with a minimum around August, and increased again in the autumn. Average CP concen-

tration in the summer of 1991 was higher (13%) than in 1989 or 1990 (10%) because of the wetter growing conditions that summer which promoted growth.

Average P and K concentrations increased with increasing stocking density (Table 5). Similar to CP levels, P and K were also high in the spring, decreased in the summer, and increased in the autumn (Fig. 4a, 4b, 5a, and 5b). Also similar to CP, P, and K levels were higher during the summer in 1991 compared to 1990 due to the better growing conditions that year.

Concentration of Mg was highest at the high stocking density (Table 5). Unlike P and K, levels of Mg were highest in the fall and lower during the spring, but the variation during the year was small (Fig. 6a and 6b).

Calcium concentration was lower at the intermediate stocking density (Table 5). The lowest value of Ca was in the spring (Fig. 7a and 7b).

The Ca/P ratio increased as stocking density declined (Table 5) and was lowest in the spring (Fig. 8a and 8b). It was highest in the summer mainly due to declines in P concentration during this period. The K/(Ca+Mg) relationship did not show significant differences among treatments (Table 5). There was a seasonal effect on the K/(Ca+Mg) ratio, which was higher in the spring and lower in the summer (Fig. 9a and 9b).

Discussion and Conclusions

Seasonal variation in tiller density was similar to the pattern described by Tallowin (1981) for areas with wet summers. It was

Table 4. Sward density (tillers m⁻²) in spring (before flowering), summer (after flowering) and autumn in 1991.

Species	Spring	Species Summer	C	Sig.
	------(Tillers m ⁻²)-----			
Total	2058a±10485	10067b ±1673	8254b±1297	**
Sown:				
<i>Lolium perenne</i>	2907a± 771	2502a ± 542	1010b± 242	*
<i>Trifolium repens</i>	1046 ± 1321	283 ± 194	827 ± 686	ns
Total	3954a± 2036	2785ab± 730	183b± 508	ns
Volunteer:				
<i>Plantago lanceolata</i>	923ab± 110	651a ± 159	1595b± 509	*
<i>Holcus lanatus</i>	3207a ± 122	2678b ± 146	434c± 226	***
<i>Dactylis glomerata</i>	340 ± 164	123 ± 24	96 ± 72	ns
<i>Agrostis</i> sp	1659 ± 753	2801 ± 782	3011 ± 180	ns
<i>Bellis</i> sp	4075 ± 6862	119 ± 47	156 ± 96	ns
<i>Poa</i> sp	3567a ± 3085	573b ± 192	275b± 187	*
<i>Geranium molle</i>	1918 ± 3207	103 ± 160	10 ± 10	ns
Total	16631a±10122	7281b ± 979	6417b± 866	*
Dead matter (%)	13.33a± 2.42	12.15a ±5.34	5.07b± 1.26	*
Bare soil (%)	53.67±23.0	44.51 ±3.91	44.42 ±11.21	ns

ns: not significant; *: p<0.05; **: p<0.01; ***: p<0.001

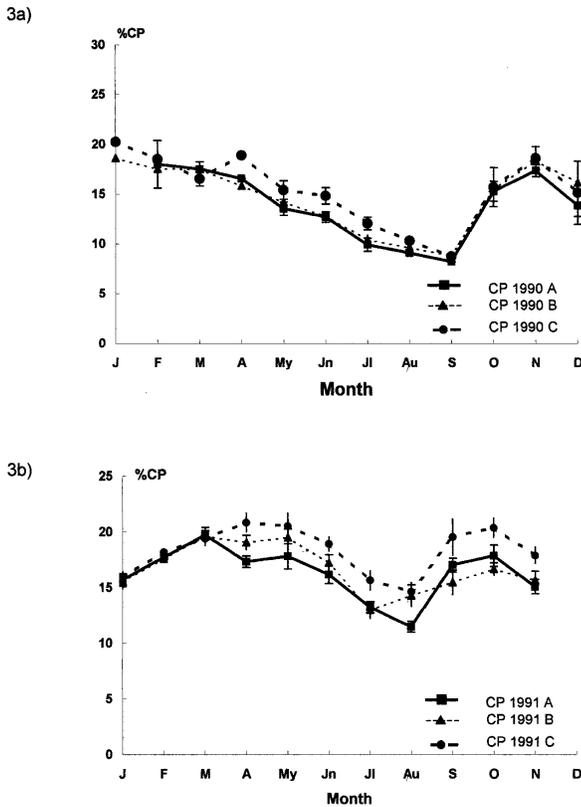


Fig. 3. Seasonal distribution of crude protein (CP) for the treatments A, B, and C, in 1990 and 1991.

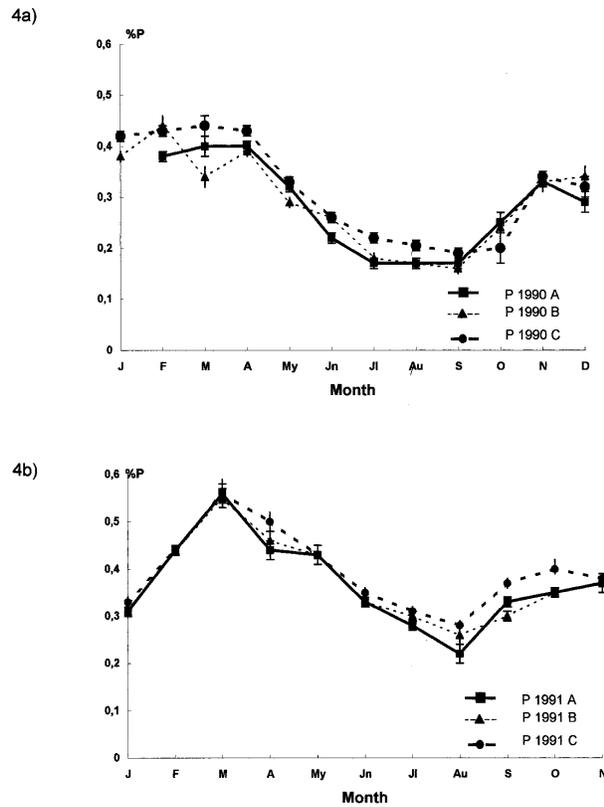


Fig. 4. Seasonal distribution of P for the treatments A, B, and C, in 1990 and 1991.

high in the spring and decreased in the summer and autumn. Patterns in seasonal variation in tiller density depend on species present (Hume and Lucas 1987, Garwood 1969, Takasaki et al. 1989). The majority of the species present in our study had their highest tiller density in spring (*L. perenne*, *T. repens*, *H. lanatus*, *D. glomerata*, *B. perenne*, *P. annua* and *G. molle*). Although others, such as *P. lanceolata*, were higher in the fall.

Similar to that described by previous authors (Curll and Wilkins 1985, Baker and Leaver 1986, Hunt 1989, Tallwin 1981, L' Huillier 1987, Xia et al. 1990),

increasing stocking density resulted in increased tiller density.

Reductions in ADF values as stocking density increased in this study are similar to what has been found in other studies (Stockdale and King 1980, Freer 1960, Gordon 1973, Castle et al. 1968, Mayne et al. 1987, Kristensen 1988, Rugambwa et al. 1990). This was a function of reduced flowering and lowering of the stem to green leaf ratio in the herbage (Munro and Walters 1985, Holmes 1989, Mott 1983).

Little dead material was accumulated in any season and treatment in this experiment due to the relatively high grazing

intensity found at all stocking density treatments. This accounts for the similar ADF values for stocking density treatments.

Seasonal variation in ADF is dependent on the development state of pasture species. Generally, as plants mature ADF increases (Minson 1982, Demarquilly 1989, Holmes 1987, Munro and Walters 1985, Corral 1974, Valdés et al. 1991). This accounts for the higher ADF values after flowering.

Protein content found was within the typical range for temperate-type grassland vegetation (Demarquilly 1989). Crude protein levels increased as stocking densi-

Table 5. Acid detergent fiber (ADF), crude protein (CP), calcium (Ca), potassium (K) and magnesium (Mg) pasture content average and relationships Ca/P (%) and K/(Ca + Mg) (milliequivalents/milliequivalents) of 3 years in each treatment and period (1: before flowering, 2: after flowering and 3: autumn) with their standard deviation.

Variable	Treatment			Sig.	Period			Sig.
	A	B	C		1	2	3	
	-----(-)-----				-----(-)-----			
ADF	26.26±3.84	26.13±3.97	25.64±4.59	ns	23.05b±2.69	28.28a±4.09	27.16a±3.30	***
CP	14.99b±3.82	15.66b±4.03	17.44a±4.75	***	18.38a±3.40	14.47b±4.09	17.89a±4.08	***
P	0.32b±0.10	0.32b±0.10	0.35a±0.10	***	0.44a±0.09	0.28b±0.08	0.33c±0.06	***
Ca	0.98a±0.31	0.92b±0.29	0.96ab±0.30	*	0.90a±0.32	0.92a±0.25	1.06b±0.34	***
K	2.23b±0.74	2.31b±0.82	2.51a±0.81	***	2.79a±0.75	2.07b±0.77	2.49c±0.76	***
Mg	0.17b±0.05	0.17b±0.04	0.18a±0.04	**	0.17b±0.03	0.18a±0.04	0.19a±0.05	***
Ca/P	3.49a±1.65	3.17b±1.51	2.90c±2.96	***	2.16a±0.88	3.59b±1.51	3.33c±1.26	***
K/(Ca+Mg)	0.98±0.47	1.03±0.45	1.08±0.47	ns	1.33a±0.55	0.91b±0.38	0.99c±0.39	***

Sig: significance; ns: not significant; *: p<0.05; **: p<0.01; ***: p<0.001

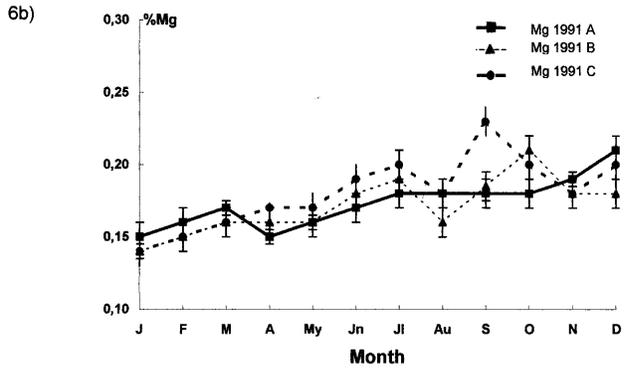
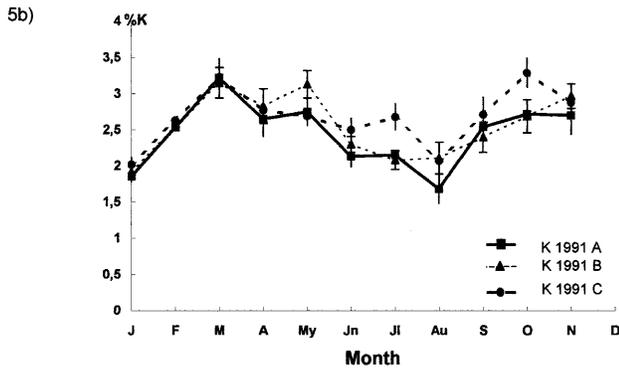
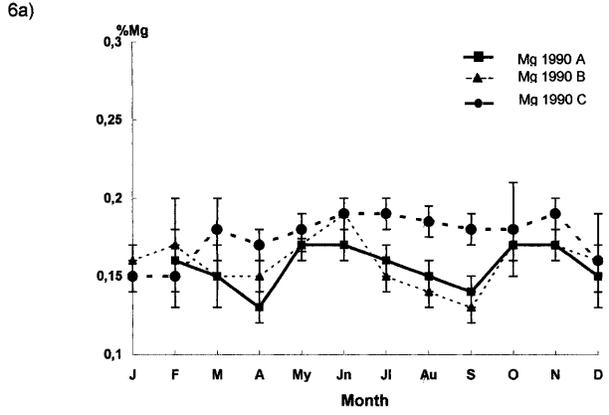
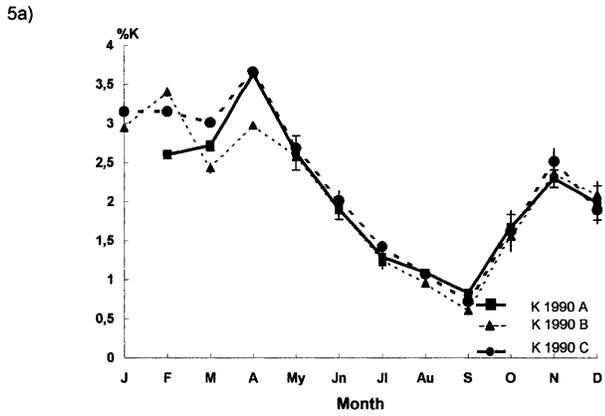


Fig. 5. Seasonal distribution of K for the treatments A, B, and C, in 1990 and 1991.

Fig. 6. Seasonal distribution of Mg for the treatments A, B, and C, in 1990 and 1991.

ty increased. Short re-growth intervals and high grazing intensity, that is to say high stocking density, increase the protein content in the pastures, because flowering is reduced. This increases the leaf to stem ratio in herbage (Stockdale and King 1980, Overman and Wilkinson 1990, Castle et al. 1968). Since the protein content of leaves is greater than that in stem (Norton 1982, Demarquilly 1989), average protein content of the forage increases. However, the protein offered to cows did not differ among treatments, because Treatment A had higher amounts of forage on offer than Treatments B or C.

Crude protein levels were highest in spring and lowest in summer because post-flowering plants had less protein content than pre-flowering plants (Munro and Walters 1985, Metson and Saunders 1978b, Roberts 1987, Stehr and Kirchgessner 1976).

Herbage mineral content found was within the typical range for temperate type grassland vegetation (Grace 1983a, 1983b, 1983c, Pickard 1986), and mineral levels of grassland were always above the minimum limits recommended for dairy cows (NRC 1989, ARC 1991). Increasing stock-

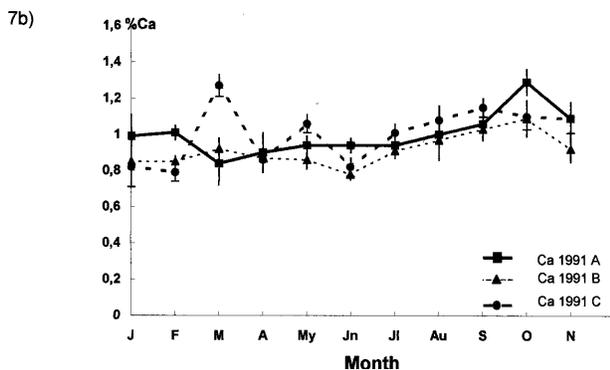
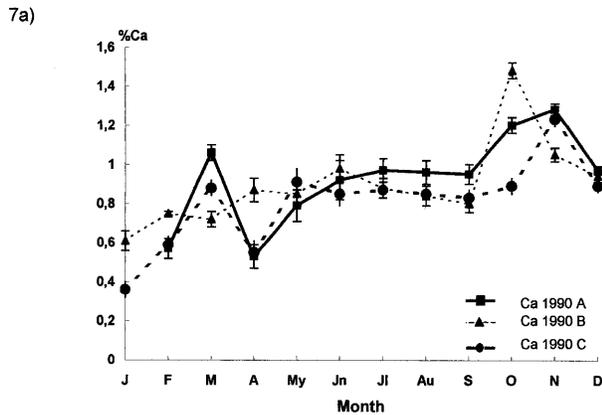


Fig. 7. Seasonal distribution of Ca for the treatments A, B, and C, in 1990 and 1991.

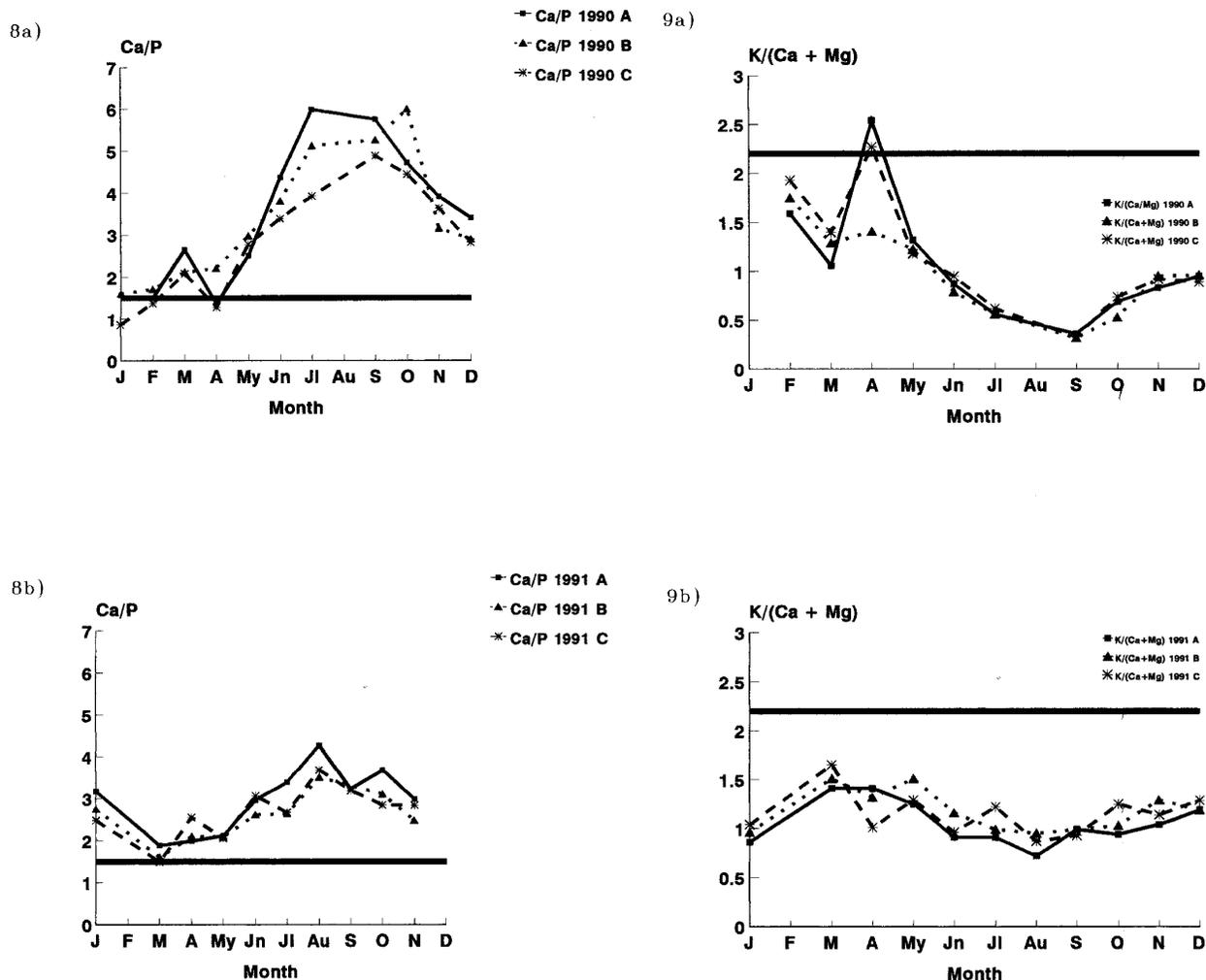


Fig. 8. Seasonal distribution of Ca/P for the treatments A, B, and C, in 1990 and 1991. Solid line indicates adequate value for animal intake described by Grunes and Allaway (1985).

Fig. 9. Seasonal distribution of K/(Ca+Mg) for the treatments A, B, and C, in 1990 and 1991.

ing density did increase the mineral content of pasture, because as for ADF and CP, development stage and age of pasture species affects mineral content of the herbage. More intensive management as higher stocking rates also introduced more quantity of nitrogen and mineral elements (eg. potassium) in the soil mainly through faeces, which usually increase soil contamination and recycling of nutrients. In the present experiment, P and K concentration decreased during the spring period as the plants approached flowering, as found by Andrieu et al. (1989), Norton (1982), Stockdale and King (1980) and Roberts (1987). In the summer P and K concentration were lower than in the other periods due to high temperatures and low rainfall which originated no leafy pasture and therefore an old pasture as found (Willman et al. 1994).

Magnesium and Ca varied little during the year as described by Roberts (1987), Metson and Saunders (1978a) and Golob and Cop (1990). Although, Mg and Ca levels were significantly lower in the spring than in the autumn.

Older recommendations indicate that the Ca/P for grazing animals should be around 1.5 and within a range of 1–2 (Grunes and Allaway 1985, Gallego 1986). In the present experiment, the upper limit was exceeded throughout the year but no osteomalacia found (Grunes and Allaway 1985). The latest A.R.C. review ARC (1991) said that concerns with upper limits were incorrect, because ruminants tolerate a great variation of Ca/P ratios.

The K/(Ca+Mg) ratio is indicative of pasture tetany. If this ratio is higher than 2.2, problems of hypomagnesemia could appear (Kemp and T'Hart 1957, Butler

1963, Metson et al. 1966). In the present experiment, most of the time this relationship was not exceeded except in the spring of 1990, but no case of hypomagnesemia was found. This was probably because the animals were being fed concentrates (2.5 kg cow day⁻¹) during the spring.

Previous small plot studies carried out in Galicia indicated that the K/(Ca+Mg) ratio was always below 1.5 (Garcia et al. 1986) and that hypomagnesemia should not be a problem. Later surveys of dairy pastures showed that this recommended value could be exceeded during the spring, but that the feeding of concentrates rich in magnesium would be sufficient to correct the imbalance in the animals diet.

In our experiment (with medium level of soil fertility), stocking density had an important effect on tiller density but did not affect the botanical composition of the

pastures. Higher stocking density increased the chemical quality of herbage. The Ca/P relationship was not a good indicator of osteomalacia, because even when the recommended values were exceeded no problems occurred. It was possible to prevent hypomagnesemia problems by feeding Mg rich concentrates to the cows during the spring.

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Grassland fire effects on corroded barbed wire

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Abstract

Fire effects on rangeland ecosystems have been studied extensively. Few studies have investigated effects of fire on rangeland developments. Only 1 study has investigated the effects of fire on barbed wire with an intact coating of corrosion-resistant zinc and no studies have investigated wire that has lost the protective coating. A common perception is that grass fire causes older wire to break more easily and become more brittle. In the present study, we determined the influence of grassland fire on wire that was 20 and 30-years old and had sufficient loss of the zinc coating to have undergone corrosion of the underlying steel. We found that regardless of age, wire subjected to grass fire did not differ ($P > 0.05$) in breaking strength, elongation, or ductility from the same wire that was not subjected to fire. We conclude that the problems experienced when repairing breaks in old barbed wire are not a result of fire, but rather brittle and weak wire resulting from exposure to the corrosive elements of the environment.

Key Words: Fence, prairie fire, Oklahoma

The results of numerous studies are available from throughout the world on the response of rangeland ecosystems to fire. Fencing is a rangeland development with potential exposure to fire. However, little is known of fire effects on fencing except for influences on preservative-treated wood posts (e.g., McCarthy et al. 1972, Evans et al. 1994) and our recent research on the effects of grassland fire on barbed wire (Engle et al. 1998). The effects of fire on barbed wire are important to rangeland managers because of the amount of wire exposed to wildfire and because the effects of fire on barbed wire are often viewed as a major limitation to implementing prescribed burning on rangelands.

Most rangeland fence is constructed of 2-point or 4-point, double-stranded, zinc-coated barbed wire that is labeled and marketed according to quality standards specified by the American Society for Testing and Materials (ASTM 1995). The American Society for Testing and Materials has published 12 and 20-year long-term studies of the effects of various environments and climates on barbed wire (Reinhart 1961, Kelly 1975), but has not investigated the effects of fire. Other than our recent research (Engle et al. 1998), no formal studies to our knowledge have been conducted to determine rangeland fire effects on barbed wire or other galvanized fencing materials commonly used on rangelands. Engle et al. (1998) determined that even 6 grass fires did

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Resumen

Los efectos del fuego en los ecosistemas de pastizal se han estudiado extensivamente, pero pocos estudios han investigado los efectos del fuego en la infraestructura del pastizal. Solo un estudio ha investigado el efecto del fuego en el alambre de p'as con una capa intacta de anticorrosivo a base de zinc, y no hay estudios que investiguen el efecto del fuego en alambre que ha perdido esta capa protectora. Una precepción com'n es que el fuego causa que el alambre viejo se rompa mas f'cilmente y llegue a ser mas r'gido. En el presente estudio determinamos la influencia del fuego en alambre de 20 y 30 a'os de edad que hab'aa perdido suficiente cubierta protectora de zinc para tener corrosi'n. Encontramos que independientemente de la edad, la resistencia a la ruptura, elongaci'n y ductibilidad del alambre sujeto al fuego no difiere ($P > 0.05$) del alambre en igualdad de condiciones pero no sujeto a fuego. Concluimos que los problemas experimentados durante la reparaci'n de rupturas de alambres viejos de p'as no son el resultado del fuego, sino mas bien, la rigidez y debilidad del alambre resultan de su exposici'n a los elementos corrosivos del ambiente.

not adversely affect the breaking strength or zinc coating of Class 1, 12 1/2 gauge barbed wire that still had a protective coating of zinc when first subjected to a grassland fire. This contradicted the common perception that grassland fire, either by reducing strength or by removing the corrosion-resistant zinc coating, reduces the life of galvanized barbed wire.

Another common perception is that grassland fire causes older wire to break more easily (i.e., loses tensile strength) and become more brittle (i.e., loses ductility). If so, wire would break more readily when stretched or when wrapped to splice a break. Hence, our objective in this study was to determine the influence of grassland fire on older wire that had sufficient loss of the zinc coating to have undergone corrosion of the underlying steel. Specifically, we determined the influence of grassland fire on breaking strength, elongation, and ductility of old, corroded wire in use in still serviceable barbed wire fence.

Methods and Materials

We collected 75-cm sections of 12 1/2-gauge, 2-point, double-stranded barbed wire from fence with minimum ages of 20 and 30 years and from newly manufactured, unused ASTM Class 1 wire. Used wire was collected in the spring and summer of 1997 in Payne County, Okla., USA, from fence constructed of new wire in 1968 and 1978. None of this wire had been subjected to fire before this study. Both the 20 and 30-year-old wire displayed complete loss of the protective zinc layer, and extensive corrosion

Table 1. Fine fuel loading and behavior of fires at three locations in tallgrass prairie to test effects on barbed wire. Values for fuel load are the mean (SE) of 10 samples. Values for fire intensity and heat per unit area were the observed behavior of 1 fire run at each location and were calculated from rate of spread estimated by 2 observers.

Location	Fuel load (kg ha ⁻¹)	Fire intensity (kW m ⁻¹)	Heat per unit area (kJ m ⁻²)
1	2,640 (100)	1,260	3,900
2	4,920 (600)	2,370	7,340
3	5,320 (170)	4,360	7,850

of the steel was visible. Pitting of the 30-year-old wire was visually observed to be deeper and more extensive than on the 20-year-old-wire. Additional wire samples were obtained from newly manufactured unused rolls of ASTM Class 1 barbed wire.

A subset of the wire was subjected to fires located in tallgrass prairie fuels and burned 4 November 1997 in the early dormant season. Three sections of wire from each treatment (unused, 20-year old, and 30-year old) were attached, unstretched, with wire clips to steel T-posts at three topographically level locations in a 65-ha pasture within a tallgrass prairie (n=9). Fine fuel load varied among locations as a result of differences in site potential and differential grazing by cattle (Table 1). Each section of wire was positioned 60 cm above the soil surface. This corresponds to the typical height of the second wire in a fence and within the zone of peak temperatures measured in previous fires in similar tallgrass prairie fuels at this same study location (Engle et al. 1989, Bidwell and Engle 1991). At each location, a headfire was ignited upwind about 5 m and allowed to spread into the area where the wire was positioned. Fuel loading and fire behavior (Table 1) were comparable to fires in tallgrass prairies burned at other dates (Engle et al. 1989, Engle et al. 1990, Bidwell and Engle 1992, Engle et al. 1993). A second subset of wire was used as a nonburned control (n=6).

After the fires, the double-stranded wire was separated into single strands and the barbs removed. A 30-cm subset (n=6) of the single strands of wire was tested for breaking strength according to ASTM A 121-92a for zinc-coated (galvanized) steel barbed wire (ASTM 1995). Oklahoma Steel and Wire Co., Inc. of Madill, Okla, USA, conducted tests of breaking strength and permanent elongation. Elongation is the increase in length of the fractured wire specimen expressed as a percentage of the original length of the wire before subjecting it to the test for breaking strength. We used elongation as a surrogate for the wire to undergo stretching before breaking.

Elongation was tested according to ASTM A 370 A4.4 for round wire. A second set (n=9) of the single strands of wire was subjected to the wrap test, a test for ductility, following the procedure outlined in ASTM A 370 A4.7 (ASTM 1995). The test consists of coiling the wire in a closely spaced helix against a mandrel of 0.25 cm diameter. The wire was coiled a maximum of five times. Failure was considered as any longitudinal or transverse cracks detected by the unaided eye after the first complete turn.

Statistical comparisons of burned and nonburned samples within wire age (i.e., unused, 20-year old, and 30-year old) were made using Student's t-test. The null hypothesis was that breaking strength, elongation, and ductility of wire would not differ between wire subjected to grassland fire and wire not subjected to grassland fire within any of the age groups. Differences were considered significant at the 0.05 level.

Results and Discussion

Regardless of age, wire subjected to fire in tallgrass prairie did not differ in breaking strength, elongation, or ductility from wire

that was not subjected to fire (Fig. 1, 2, and 3). Therefore, we failed to reject our hypothesis that breaking strength, elongation, and ductility of wire would not differ between wire subjected to grassland fire and wire that was not. As galvanized steel barbed wire rusts, it loses strength and ductility after the corrosion-protective zinc coating is lost in exposure to the natural environment (Reinhart 1961, Kelly 1975). The barbed wire we collected from existing fences exhibited complete failure of the protective zinc coating. Fire did not further reduce strength, elongation potential, or ductility in spite of the advanced corrosion of the 30-year-old wire.

A common perception among rangeland managers has been that fire, either by reducing strength or by removing the corrosion-resistant zinc coating, reduces the life of barbed wire. Our recently reported research showed that even repeated grass fires did not reduce the breaking strength or corrosion resistance of 14-year old Class 1, 12 1/2 gauge barbed wire (Engle et al. 1998). Results of the present study contradict another common perception that grassland fire causes older wire to break more easily and become more brittle. The weaker and more brittle the wire, the more readily the wire will break when stretched or wrapped to splice a break.

Our results have 2 implications to barbed wire fences with advanced corrosion. First, rangeland managers often assert that they find more broken wire after grass fires. If so, a number of factors may explain this increased incidence of broken wire. Perhaps wires are broken in

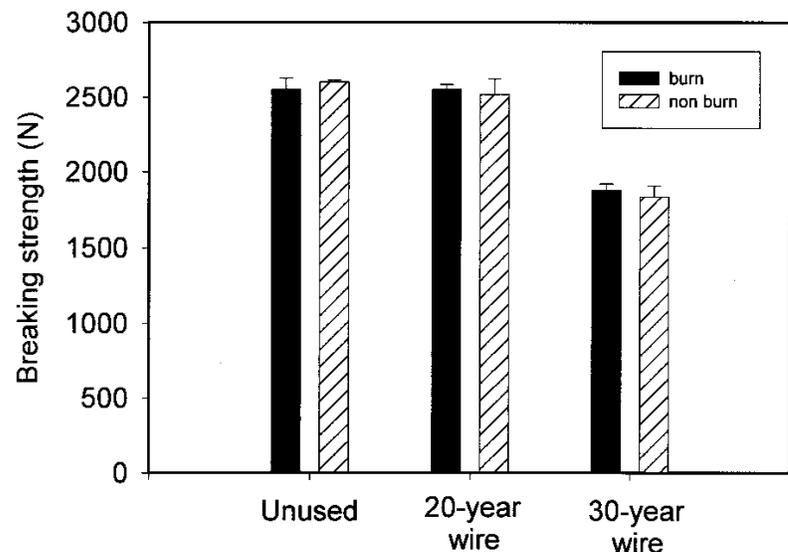


Fig. 1. Breaking strength in newtons (N) of single strands of barbed wire subjected to grassland fire. Values are means of 9 observations (burn) and 6 observations (non burn); bars are 1 standard error. Burn treatments did not differ ($P > 0.05$) for wire of any age.

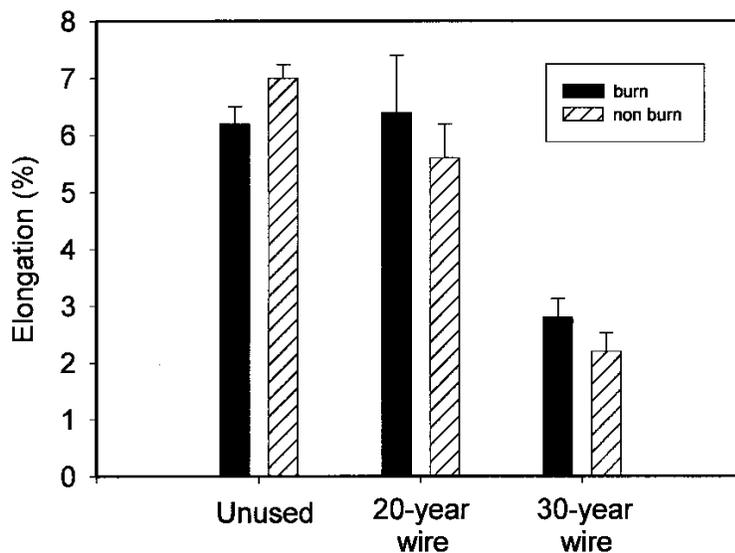


Fig. 2. Permanent elongation of single strands of barbed wire subjected to grassland fire. Values are means of 9 observations (burn) and 6 observations (non burn); bars are 1 standard error. Burn treatments did not differ ($P > 0.05$) for wire of any age.

some way in expansion and contraction during the fire, specifically at contact points such as at staples on wood posts that undergo accelerated wear from friction. Similar accelerated wear occurs at contact points for other reasons including expansion and contraction with changes in ambient air temperature. The effect of expansion and contraction on contact points could be tested under various stretching configurations, for example, across posts in curved or v-shaped configurations. We do not think placing wire under tension (i.e., stretching) would alter the results of our study because, in our

previous research (Engle et al. 1998), breaking strength of wire subjected to fire did not decrease because of stretching. In that research, we found no difference in breaking strength between stretched wire that was burned and unused wire that had never been stretched or burned.

Fire suppression or ignition activities may also be responsible for breaks in wire. We think the latter is especially probable during wildfire suppression when vehicles make unintended contact with fences. In some fuel types, already broken wires would be more easily seen after obstructing vegetation is removed in the fire. Finally,

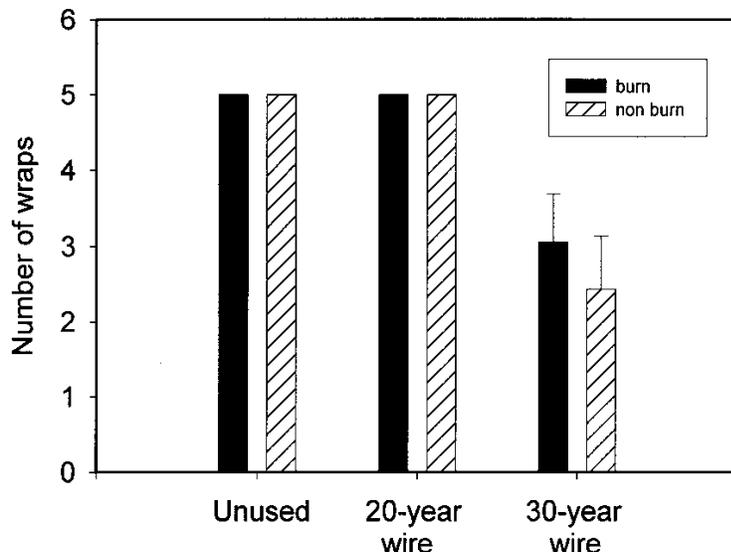


Fig. 3. Number of wraps before failure of single strands of barbed wire subjected to grassland fire. Values are means of 9 observations each for burn and non burn; bars are 1 standard error. Five turns indicates no failure. Burn treatments did not differ ($P > 0.05$) for wire of any age.

corroded wire is brittle and weak, so that when the wire breaks for any reason, repair is difficult. We conclude that the problems managers experience when repairing breaks in old wire subjected to grassland fire are not a result of fire, but rather brittle and weak wire resulting from exposure to the corrosive elements of the environment.

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Response of incomplete Tifton 9 bahiagrass stands to renovation

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Abstract

Establishment of warm-season grasses from seed is often impeded by slow germination and emergence, and low seedling vigor. Stand development can be further retarded by unfavorable soil moisture resulting from high temperatures and erratic precipitation. Management of poorly established stands of warm-season grasses has received limited research attention. Two- or 3-year old, poorly established stands (basal occupation < 61%) of 'Tifton 9' bahiagrass (*Paspalum notatum* Flüggé var. *saure*) at a dry upland site and at a moist lowland site were reseeded (5.6 kg ha⁻¹) in April of 2 different years either without tillage or after rototilling or light disking and compared to a non-seeded control. Our objective was to determine whether any combination of tillage and/or seeding would enhance stand coverage. At the upland site, basal occupation of the control increased from an initial 61 to 80%. No benefit was derived from interseeding, and both tillage treatments resulted in a stand reduction ($P < 0.05$) after 1 year. At the lowland site, basal occupation increased from an initial 28 to 59% for the control. Similar responses were observed with renovation treatments, but none were greater ($P > 0.05$) than the control. Bahiagrass stands with at least a few plants per m² should be managed to minimize weed encroachment, but introducing additional seed, with or without tillage, offered no benefit.

Key Words: establishment, reseeding, tillage, *Paspalum notatum*

Establishment of warm-season grasses is made difficult by several factors. Erratic precipitation and high temperatures at planting or soon after can lead to soil moisture conditions unfavorable for germination, emergence and seedling survival. Ries and Hoffman (1996) indicate that, in the Northern Plains, stand failures can result for any planting date in a given year. Considerable recent research has examined planting management in the Northern and Central Plains and mid-Atlantic, particularly herbicide use, in establishing several warm-season grass species including: big bluestem [*Andropogon gerardii* Vitman], sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern], prairie sandreed [*Calamovilfa longifolia* Hook.], switchgrass [*Panicum virgatum* L.], indiangrass [*Sorghastrum nutans* (L.) Nash], sideoats gramma [*Bouteloua curtipendula* (Michx.) Torr.], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and blue gramma [*Bouteloua gracilis* (H.B.K.) Lag ex Steud.]

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Resumen

El establecimiento de zacates de estación caliente a partir de semilla a menudo se dificulta por la lenta geminación y emergencia y el bajo vigor de las plántulas. El desarrollo de la población puede ser aun mas retardado por condiciones desfavorables de humedad del suelo que resultan de las altas temperaturas y la precipitación errática. La investigación sobre manejo de praderas de zacates de estación caliente establecidas pobremente ha recibido poca atención. Praderas de 'Tifton 9' 'Bahiagrass' (*Paspalum notatum* Flüggé var. *Saure*) mal establecidas (Ocupación basal < 61%) de 2 a 3 años de antigüedad y situadas en un sitio seco y uno húmedo se resembraron (5.6 kg ha⁻¹) en abril de 2 diferentes años sin practicas de labranza y después de barbechar y rastrear ligeramente el terreno y se compararon con praderas control sin resiembra. Nuestro objetivo fue determinar si alguna combinación de labranza y/o siembra mejoraría la cobertura de la pradera. En el sitio seco, la cobertura basal de las praderas control se incremento de 61% inicial a 80%. La interseembra no produjo beneficios adicionales y ambos tratamientos de labranza redujeron la cobertura de la pradera ($P < 0.05$) después de un año. En el sitio húmedo, en las praderas control, la cobertura basal aumentó del 28% inicial a 59%, se observó una respuesta similar con los tratamientos de renovación, pero ninguno fue mayor ($P > 0.05$) que el control. Las praderas de 'Bahiagrass', con al menos unas pocas plantas por m², deben ser manejadas para minimizar la invasión de maleza y la adición de semilla, con o sin practicas de labranza, no produce beneficio alguno.

(Bahler et al. 1990, Beckman et al. 1993, Hintz et al. 1998, Masters et al. 1990, McKenna and Wolf 1990, Ries and Hofmann 1996, Vassey et al. 1985, Vogel 1987).

Though total annual precipitation is greater in the southeastern U.S. than in the Great Plains, precipitation in summer can be erratic and periods of drought associated with high temperatures occur frequently enough to make warm-season grass establishment uncertain in this region as well. Bahiagrass (*Paspalum notatum* Flüggé var. *saure*), widely used for pasture in the humid southeastern U.S., germinates slowly (West and Marousky 1989) and emerged seedlings are sensitive to competition (Beaty and Powell 1978, Williams and Webb 1958). While a number of factors related to establishment, including planting date, seed treatment, dehulling, and planting rate have been considered, only extremely high seeding rate promoted more rapid establishment (Gates and Mullahey 1997, Gates and Dewald 1998). Even when every effort is made to ensure stand establishment, weather extremes may limit success. Poor establishment frequently results

in variable stands with open areas. Options in this situation include: 1) doing nothing, 2) renovation through some combination of seeding and tillage, and 3) complete seedbed preparation and reseeded—still facing the same possibility of success or failure.

While considerable effort has been directed at the initial establishment of warm-season grasses, including bahiagrass, management options to improve poor stands have not been considered. Plots consisting of relatively open stands of bahiagrass from previous research provided an opportunity to examine the response of 'Tifton 9' bahiagrass stands to renovation treatments. Experiments were conducted at different sites to determine the feasibility of interseeding x tillage combinations to improve stands of Tifton 9 bahiagrass.

Materials and Methods

Experimental sites used in this research were previously planted in 1993 (upland site) and 1995 (lowland site) to determine establishment response of Tifton 9 bahiagrass to several planting variables and seed treatments (Gates and Mullahey 1997, Gates and Dewald 1998). Upon completion of these experiments, relatively open 2- or 3-year old stands provided an opportunity to examine treatments which might enhance stand coverage. The 2 sites at the Coastal Plain Experiment Station in Tifton, Ga. (31° 26' N, 83° 35' W) were a droughty upland (Dothan loamy sand; fine-loamy siliceous thermic Plinthic Kandiudults) with unfavorable surface soil moisture during much of the growing season and a lowland site (Alapaha sand; loamy, siliceous, thermic Arenic Plinthic Paleaquults) where heavier soil texture and physiographic position resulted in more favorable surface soil moisture (Gates and Dewald 1998).

Four treatment combinations of tillage and reseeded were evaluated at both sites: 1) rototilling to a depth of ~100 mm, resulting in nearly complete sod destruction, followed by seeding, 2) shallow disking, resulting in disturbance of less than half of the sod, followed by seeding, 3) interseeding alone, and 4) undisturbed, non-seeded control. Six replications were planted on 10 April 1995 at the upland site. At the lowland site, 4 replications were planted 13 April 1998. All planting was done at the same seeding rate (5.6 kg ha⁻¹) using a 7-row plot drill equipped with fluted coulters and double disk openers spaced 178 mm apart. Soil conditions at

the time of planting at both sites allowed penetration and seed placement at a depth of ~15 mm. A firm seedbed was provided by driving a tractor across the plots before and immediately after planting. Nitrogen fertilizer was applied (56kg ha⁻¹) once in spring at each site. Soil tests indicated other nutrients were adequate. Plots were mowed periodically during the growing season. No herbicide applications were made. Treatments were assigned to plots without regard to previous treatment, encompassing several plots from previous experiments. Plot size was 1.5 x 20 m at the upland site and 1.5 x 9.1 m at the lowland site.

Initial stand ratings were taken at the upland site during the week preceding replanting treatments. On 3 April 1995, presence or absence of bahiagrass was recorded in each 100 square cm unit of a 1 m x 1 m sampling quadrat, using 9 randomly placed quadrats per plot. Stand ratings were repeated the following spring, 11 May 1996, to evaluate change in stand ratings. At the lowland site the same procedure was used except that 5 quadrats per plot were used. Initial stands were evaluated 7 April 1998 and final stands on 10 May 1999.

Initial and final stand ratings and the change in rating were analyzed using analysis of covariance implemented using SAS GLM (SAS 1998). The statistical model evaluated final stand ratings, adjusted using initial stand as a covariate. Treatment means were compared using single degree of freedom contrasts. Tillage treatments (rototilling and disking) were first contrasted with treatments without tillage (control and interseeding). Two additional contrasts compared the 2 treatments within each tillage category (rototilling vs. disking; control vs. interseeding).

Results and Discussion

Bahiagrass stands were 2 years old at the upland site and 3 years old at the lowland site when treatments were initiated. Basal occupation averaged 61% initially at the upland site but only 28% at the lowland site. Final stands (averaging 70% at the upland site; 62% at the lowland site) were similar, indicating more rapid increase in cover with more favorable soil moisture conditions at the lowland site. Final stand occupation at the upland site was lower ($P < 0.05$) for treatments including tillage compared to those without tillage (Table 1). A decrease in basal occupation due to rototilling indicated substantial sod destruction, resulting in lower ($P < 0.05$) final stands compared with disking. No difference ($P > 0.05$) in final basal occupation resulted from interseeding or control. The similarity in response of the latter treatments strongly indicates that drilling with 5.6 kg ha⁻¹ of additional seed made no contribution to stand improvement at this site.

At the lowland site (Table 1) there was a marked improvement in stands, however, no differences were detected between any of the treatments and the control. The positive change observed for rototilling plus interseeding at the lowland site contrasted sharply with the response to this treatment at the upland site. More favorable soil moisture holding capacity and greater spring precipitation in 1998 compared with 1995 (Fig. 1) may have contributed to more successful establishment of newly planted seed.

Tifton 9 bahiagrass stands, relatively free of perennial weeds, with basal occupation ranging between 20 and 60%, as evaluated in this research, did not benefit from any combination of tillage and/or reseeded. Even the most open stands had several established plants within a 1.0 m² quadrat. Under these conditions, the best

Table 1. Least squares means and F-test probabilities associated with single d.f. contrasts for final basal occupation of Tifton 9 bahiagrass stands following tillage and reseeded treatments at 2 sites near Tifton, Ga.

Treatment	Dry Upland Site	Moist Lowland Site
	------(No)-----	
Interseed	78	60
Disk	68	52
Rototill	55	78
Control	80	59
Contrast	----- P > F -----	
Tillage vs None	<0.0001	0.62
Disk vs Rototill	0.007	0.10
Interseed vs Control	0.63	0.94

Number of 100 x 100 mm squares occupied by bahiagrass out of 100 possible within 1 m² quadrat.

recommendation is to allow stands to fill in from established plants. Interplant distances of less than 1 m established an environment in which seedlings apparently were unable to compete successfully enough with established plants to improve the rate of stand coverage. However, it is also likely that, at the scale of a field planting, if interplant spaces approach a few meters, it will require several years for the stand to become completely covered without introducing additional seed.

Tifton 9 has a more erect morphology than the more widely used cultivar 'Pensacola' (Gates et al. 1999). Werner and Burton (1991) found that a single Pensacola seedling could occupy an area 1.2 times that of a Tifton 9 seedling in a single growing season in a spaced planting. Our observations suggest that once Pensacola seedlings are established, a stand may cover more rapidly than with Tifton 9.

The slow rate of bahiagrass establishment and the difficulty in improving stands after initial planting underscores the need to develop strategies to improve the reliability of rapid establishment of bahiagrass from seed. This is especially critical with Tifton 9 to capitalize on the potential yield advantages of this improved cultivar (Burton 1989, Gates et al. 1999).

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Predictive equations for biomass and fuel characteristics of Argentine shrubs

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Abstract

Predictive equations for estimating shrub biomass in semi-arid scrub ecosystems are essential for evaluating shrub encroachment, conducting ecosystem-level studies of net primary productivity (NPP) and nutrient cycling, and examining effects of different fire regimes. In this study, we developed predictive equations to estimate total aboveground biomass and biomass of foliage and stems of the 8 most common shrubs in the semi-arid scrub (Monte) of central Argentina. We also examined the relationship between shrub size and proportions of these components for the dominant species, *Larrea divaricata* Cavanilles (creosotebush), and determined fuel characteristics (dead-to-live ratio, bulk density) of the 8 shrub species. Regression analyses were used to examine the relationships between aboveground biomass and 5 field measurements (diameter of the longest stem, shrub height, maximum crown width, crown width at right angles to maximum crown width, and crown volume). A natural log-log model based on a single variable best described this relationship in most cases. The easiest field measurement for 6 of the 8 species was diameter of the longest stem, and this measure was often the best predictor of shrub biomass. As *L. divaricata* increased in size, the proportional biomass of large stems increased, and biomass of foliage and small stems decreased. This pattern suggests productivity may decrease with shrub age. The mass of dead material was low in most shrub species. Bulk densities were comparable to those of shrubs in other semi-arid ecosystems. Equations developed here will allow rapid and accurate estimation of shrub biomass in the Monte of Argentina.

Key Words: Semi-arid scrub, *Larrea*, shrub biomass, Monte, Argentina

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Resumen

Las ecuaciones predictivas para estimar la biomasa de arbustos en ecosistemas semiáridos son esenciales para evaluar incrementos en la densidad de arbustos, para conducir estudios de productividad primaria neta (PPN) y ciclo de nutrientes y para examinar los efectos de diferentes regímenes de fuego. En este estudio se desarrollaron ecuaciones predictivas para estimar biomasa aérea total y biomasa de hojas y ramas de las 8 especies de arbustos más comunes en el arbustal semiárido (Monte) del centro de Argentina. También se examinó la relación entre el tamaño del arbusto y la proporción de cada uno de estos componentes en la especie dominante, *Larrea divaricata* Cavanilles (jarilla), y se determinaron características combustibles (proporción de muerto a vivo, densidad de la corona) en las 8 especies. La relación entre biomasa aérea y 5 medidas tomadas en el campo a los arbustos (diámetro de la rama más larga, altura, ancho máximo de la corona, ancho perpendicular al ancho máximo y volumen) fue evaluada mediante el uso de análisis de regresión. En la mayoría de los casos, el modelo logarítmico natural con una sola variable fue el que mejor describió esta relación. La medida más fácil de tomar en el campo en 6 de las 8 especies fue el diámetro de la rama más larga, la que frecuentemente fue la que mejor predijo la biomasa de los arbustos. El aumento en tamaño de *L. divaricata* fue acompañado por un aumento en la proporción de biomasa aportada por las ramas grandes, y por un descenso en la proporción de biomasa aportada por hojas y ramas pequeñas. Este patrón sugiere que la productividad de los arbustos decrecería con la edad. La cantidad de material muerto fue escasa en la mayoría de las especies. La densidad de la corona de los arbustos fue comparable a la de arbustos en otros ecosistemas semiáridos. Las ecuaciones desarrolladas aquí permitirán una estimación rápida y precisa de la biomasa de arbustos en el Monte de Argentina.

Shrubs are a major component of vegetation in semi-arid ecosystems worldwide, and their ability to dominate these systems is a matter of ecological and economic concern (Schlesinger et al. 1990). Predictive equations for estimating shrub biomass from relatively simple morphometric data collected in the field have been developed for shrubs in a variety of ecosystems (see Etienne 1989, Catchpole and Wheeler 1992 for reviews), but are generally lacking for the semi-arid Monte of Argentina (Braun et al. 1979). This ecosystem is similar to creosotebush [*Larrea tridentata* (Sesse & Moc. ex DC) Cov.] -dominated regions in North

America, and covers an area of 600,000 km², or about 16% of Argentina (Ragonese 1967). Reliable equations to estimate woody vegetation biomass are needed for evaluating rates of shrub encroachment, for estimating fuel loads for fire models and evaluating effects of various fire management regimes, as well as for ecosystem-level studies of net primary productivity (NPP) and nutrient cycling.

Our research had 3 objectives: 1) to develop predictive equations to estimate total aboveground biomass, as well as biomass of foliage and stems (grouped by diameter class) of the 8 most common shrubs in Monte of central Argentina; 2) examine the relationship between shrub size and relative proportions of components (foliage and stems) for the dominant species, *Larrea divaricata* Cavanilles (creosotebush); and 3) determine fuel characteristics (dead-to-live ratio and bulk density, i.e., biomass per unit volume occupied by biomass and air) of these 8 species.

Materials and Methods

Study Area

Shrubs were collected at Los Ranqueles Ranch (18,000 ha) located 15 km E of Lihue Calel National Park (38° 00' S, 65° 00' W) in La Pampa province, Argentina. The climate is characterized by hot summers, cool winters, and low, unpredictable rainfall (mean annual precipitation from 1983 to 1993 was 524 ± 175 mm (Dirección de Estadística y Censos 1981, 1991, Lihue Calel National Park, unpubl. data). The vegetation consists of a mosaic of shrub patches and open areas. *L. divaricata* generally comprises 80–90% of the shrub biomass; other less abundant shrubs include *L. cuneifolia* Cavanilles (jarilla macho), *Condalia microphylla* Cavanilles (piquillín), *Geoffroea decorticans* (Gill ex Hook. et Arnott) Burkart (chañar), and *Prosopis flexuosa* DC var. *depressa* F.A.

Roig (alpataco dulce) (Instituto Nacional de Tecnología Agropecuaria 1980). Open areas and the understory below shrubs consist of subshrubs [e.g., *Acantholipia seriphioides* (A. Gray) Moldenke (tomillo), *Senna aphylla* (Cay.) Irwin & Barneby (pichanilla)], grasses (e.g., *Stipa* spp.), and herbs [e.g., *Medicago minima* (L.) Grufberg (trébol de carretilla), *Erodium cicutarium* (L.) L'Herit. Ex Ait. (alfilerillo), and *Baccharis* spp.].

Shrub Sampling

Shrubs of *Chuquiraga erinacea* Don (chilladora), *C. microphylla*, *G. decorticans*, *L. cuneifolia*, *L. divaricata*, *L. nitida* Cavanilles (jarilla crespá), and *P. flexuosa* var. *depressa* were sampled during the period of maximum leaf area (late spring to early autumn) of 1993–1994 and 1994–1995. Individual plants were selected to encompass a range of heights and canopy forms observed in the field (Table 1). Saplings (individuals 3.20-m height) of the tree *Prosopis caldenia* Burkart (caldén) were also collected and treated as shrubs in this analysis. All shrubs were measured for: 1) diameter of the longest stem at 10 cm above the ground (dls) to the nearest 0.05 mm using a caliper, 2) height from ground level to the tallest living tissue (h) to the nearest 5 cm, 3) maximum crown width (mcw) to the nearest 5 cm, and 4) crown width at right angles to mcw (cw90) to the nearest 5 cm. Shrubs were then cut at ground level and placed in separate bags. Diameter of the longest stem was not measured in *C. microphylla* or *P. flexuosa* var. *depressa* because the canopy structure and abundant thorns of these species made it difficult and impractical to measure.

All shrubs were transported to the laboratory, dried at 65°C to a constant weight, and weighed to determine total biomass. A representative sample of each individual (about 25 %) was selected and separated into foliage and live and dead stems. Stems were further divided into diameter

classes representing standard time lags for equilibrating fuel moisture models as follows: <6 mm (1 hour), 6–25 mm (10 hrs), >25–76 mm (100 hrs) (Fosberg 1970, Rothermel 1972, Kessel et al. 1978, Pereira et al. 1995). All components were then weighed separately.

Data Analysis

Biomass of each component was calculated by multiplying the proportion of each component in the subsample by the total biomass of each shrub. Crown volume (vol) was calculated using the formula for the solid object that best fits the natural shape of each shrub species (Ludwig et al. 1975, Murray and Jacobson 1982, Molinero 1983, Etienne 1989) as follows: *Larrea* spp., *P. caldenia*, *G. decorticans*, and *C. erinacea*, inverted cone [$\frac{1}{3} R^2 h$, where R = radius, calculated as $(mcw + cw90)/4$]; *C. microphylla*, upper half of a spheroid ($\frac{4}{3} R^2 h$); *P. flexuosa* var. *depressa*, upper half of a prolate spheroid ($\frac{4}{3} mcw cw90h$).

Regression analyses were conducted with the statistical package SPSS (SPSS Inc. 1996) to examine the relationship between total aboveground biomass, and the biomass of each component and each of the field measurements (dls, h, mcw, cw90 and vol). The following linear models were evaluated: 1) simple linear ($y = b x$ and $y = a + b x$); 2) natural logarithmic ($y = a + b \ln(x)$); 3) natural log-log ($\ln(y) = \ln(a) + b \ln(x)$); 4) exponential ($\ln(y) = \ln(a) + b x$); and 5) multiple regression ($y = a + b_1 x_1 + b_2 x_2$ and $\ln(y) = \ln(a) + b_1 \ln(x_1) + b_2 \ln(x_2)$). The best models for each species were selected based on the maximum values of the coefficients of determination (r^2) and standard errors of the estimate ($S_{y,x}$). When more than 1 model presented similarly good fit to the data, the regression equation with the fewest parameters was chosen as the best model.

Although logarithmic models often are used to predict biomass of shrubs from

Table 1. Number of individuals, ranges of measurements [dry weight (w), volume¹ (vol.), and height (h)] and mean values ± SE of bulk density (ψ_b) and dead to live ratio (dl) of each species.

Species	n	w (g)	vol (ms ³)	h (m)	b (g m ⁻³)	d/l
<i>C. erinacea</i>	10	90.5 – 5026.2	0.02 – 1.09	0.40 – 1.10	4955.4 ± 400.9	0.02 ± 0.01
<i>C. microphylla</i>	15	25.8 – 41326.1	0.02 – 43.28	0.20 – 2.40	1785.0 ± 163.8	0.02 ± 0.01
<i>G. decorticans</i>	15	11.2 – 11228.3	0.001 – 2.48	0.20 – 2.70	4854.8 ± 511.7	0.02 ± 0.01
<i>L. cuneifolia</i>	15	17.6 – 10503.7	0.02 – 5.79	0.40 – 2.30	2285.8 ± 224.1	0.01 ± 0.00
<i>L. divaricata</i>	30	63.4 – 24085.0	0.03 – 20.17	0.55 – 3.30	1324.1 ± 77.9	0.01 ± 0.00
<i>L. nitida</i>	15	49.4 – 31923.3	0.03 – 16.83	0.45 – 2.85	1671.2 ± 100.5	0.04 ± 0.01
<i>P. caldenia</i>	15	89.3 – 14257.5	0.06 – 7.54	0.50 – 3.20	1396.9 ± 115.8	0.01 ± 0.00
<i>P. flexuosa</i> var. <i>depressa</i>	15	107.6 – 19705.2	0.49 – 94.00	0.30 – 2.00	158.7 ± 11.3	0.17 ± 0.04

Table 2. Best fit linear equations and power equations for predicting total aboveground biomass, foliage biomass, and biomass of stems by diameter class (<6, 6–25, > 25 mm) for 8 woody species. $S_{y,x}$ = standard error of the estimate for linear equations ($S_{y,x1}$), back-transformed values from log-log models ($S_{y,x2}$), and power equations ($S_{y,x3}$); r^2 = coefficient of determination for linear equations (r_1^2) and power equations (r_2^2); w = dry weight (g); vol = volume (m^3); dls = diameter of the longest stem at 10-cm height (mm); mcw = maximum crown width (m); cw90 = crown width at right angles to mcw (m); h = height (m); ln = natural log. Total biomass equations using dls are presented for all species in which this variable was measured, even though this was not always the best predictor, because dls is the easiest variable to measure and is a good predictor of biomass. All models are significant at $p < 0.005$.

Species	n	Biomass	Best fit linear equation	$S_{y,x1}$	$S_{y,x2}$	r_1^2	Power equation	$S_{y,x3}$	r_2^2
<i>C. erinacea</i>	10	Total	$\ln(w) = 6.55 + 2.55 \ln(mcw)$	0.28	513.66	0.95	$w = 786.93 mcw^{2.31}$	502.03	0.91
			$\ln(w) = 1.11 + 2.21 \ln(dls)$	0.84	1084.83	0.56	$w = 30.99 dls^{1.46}$	922.66	0.68
	10	Leaves	$\ln(w) = 6.80 + 0.96 \ln(mcw)$	0.29	286.87	0.84	$w = 899.47 mcs^{1.04}$	281.63	0.80
		< 6 mm	$\ln(w) = 5.70 + 1.34 \ln(cw90)$	0.32	103.10	0.92	$w = 292.70 cw90^{1.44}$	103.28	0.81
<i>C. microphylla</i>	15	Total	$\ln(w) = 6.77 + 2.93 \ln(mcw)$	0.29	5592.90	0.98	$w = 1692.02 mcw^{2.24}$	2374.36	0.96
			$\ln(w) = 5.04 + 2.19 \ln(mcw)$	0.23	162.74	0.98	$w = 116.42 mcw^{2.43}$	160.62	0.98
	15	< 6mm	$\ln(w) = 6.39 + 2.40 \ln(cw90)$	0.35	572.30	0.95	$w = 342.58 cw90^{2.82}$	345.65	0.99
		6–25 mm	$w = -2448.99 + 3578.03 cw90$	653.98		0.96			
<i>G. decorticans</i>	15	Total	$\ln(w) = -2.15 + 2.64 \ln(dls)$	0.32	886.67	0.98	$w = 0.41 dls^{2.31}$	406.15	0.99
			$\ln(w) = 3.71 + 2.60 \ln(h)$	0.46	51.20	0.92	$w = 43.27 h^{2.65}$	42.63	0.97
	15	< 6 mm	$\ln(w) = 5.15 + 2.80 \ln(h)$	0.33	577.41	0.96	$w = 318.40 h^{1.80}$	283.82	0.86
		6–25 mm	$\ln(w) = -4.17 + 2.96 \ln(dls)$	0.24	348.83	0.99	$w = 0.07 dls^{2.58}$	276.72	0.96
<i>L. cuneifolia</i>	15	Total	$\ln(w) = 6.99 + 0.90 \ln(vol)$	0.29	428.87	0.92	$w = 1149.97 vol^{0.65}$	360.00	0.79
			$\ln(w) = -0.60 + 2.72 \ln(dls)$	0.47	1804.25	0.93	$w = 6.73 dls^{1.94}$	613.85	0.95
	15	Leaves	$\ln(w) = 5.69 + 0.60 \ln(vol)$	0.33	135.93	0.93	$w = 233.83 vol^{0.81}$	79.11	0.97
		< 6 mm	$\ln(w) = 6.45 + 0.77 \ln(vol)$	0.36	367.91	0.95	$w = 677.67 vol^{0.63}$	219.63	0.94
<i>L. divaricata</i>	14	6–25 mm	$\ln(w) = 7.05 + 1.16 \ln(vol)$	0.53	3024.72	0.95	$w = 1670.55 vol^{0.70}$	372.93	0.98
			Total	$\ln(w) = 7.19 + 0.93 \ln(vol)$	0.32	2423.82	0.96	$w = 1410.32 vol^{0.94}$	2307.43
	30	Leaves	$\ln(w) = -0.72 + 2.71 \ln(dls)$	0.44	3731.82	0.93	$w = 6.11 dls^{2.03}$	3509.81	0.70
			$\ln(w) = 4.40 + 1.68 \ln(cw90)$	0.54	211.19	0.83	$w = 88.51 cw90^{1.77}$	200.89	0.66
<i>L. nitida</i>	15	Total	$\ln(w) = 5.37 + 1.93 \ln(cw90)$	0.43	419.71	0.91	$w = 285.02 cw90^{1.61}$	405.18	0.76
			$\ln(w) = 6.49 + 1.24 \ln(vol)$	0.43	1036.75	0.96	$w = 764.32 vol^{1.11}$	1142.68	0.89
	11	> 25 mm	$\ln(w) = 5.03 + 1.15 \ln(vol)$	0.65	794.16	0.62	$w = 70.43 vol^{1.60}$	607.11	0.80
			Total	$\ln(w) = 7.39 + 0.99 \ln(vol)$	0.26	3221.38	0.99	$w = 12.14 vol^{2.74}$	4185.39
<i>P. caldenia</i>	15	Total	$\ln(w) = -0.76 + 2.77 \ln(dls)$	0.60	2676.48	0.92	$w = 0.30 dls^{2.85}$	2203.00	0.94
			$\ln(w) = 4.46 + 1.97 \ln(mcw)$	0.50	131.24	0.85	$W = 89.61 MCW^{1.95}$	130.54	0.91
	15	< 6 MM	$\ln(w) = 6.18 + 0.83 \ln(vol)$	0.29	270.20	0.96	$w = 386.34 vol^{0.83}$	141.11	0.96
		6–25 mm	$\ln(w) = 6.86 + 1.30 \ln(vol)$	0.40	2451.62	0.97	$w = 1389.00 vol^{0.88}$	380.75	0.98
<i>P. flexuosa</i> var. <i>depressa</i>	15	Total	$\ln(w) = -0.43 + 2.18 \ln(dls)$	0.28	1200.28	0.97	$w = 0.08 dls^{2.68}$	1030.40	0.93
			$\ln(w) = 5.27 + 0.88 \ln(vol)$	0.33	67.64	0.94	$w = 219.94 vol^{0.84}$	62.89	0.89
	15	< 6 mm	$\ln(w) = -0.32 + 1.85 \ln(dls)$	0.27	267.93	0.96	$w = 106 dls^{1.76}$	267.85	0.85
		6–25 mm	$\ln(w) = 5.84 + 2.85 \ln(cw90)$	0.41	517.63	0.93	$w = 220.83 cw90^{3.78}$	412.51	0.89
<i>P. flexuosa</i> var. <i>depressa</i>	8	> 25 mm	$\ln(w) = 5.75 + 1.98 \ln(vol)$	0.45	288.08	0.87	$w = 373.91 vol^{1.75}$	238.78	0.96
			Total	$\ln(w) = 6.24 + 2.63 \ln(cw90)$	0.32	2313.61	0.96	$w = 208.02 cw90^{3.60}$	1893.13
	15	Leaves	$\ln(w) = 3.19 + 0.85 \ln(vol)$	0.40	160.33	0.95	$w = 61.99 vol^{0.61}$	117.51	0.91
			< 6 mm	$\ln(w) = 4.52 + 0.98 \ln(vol)$	0.27	1240.57	0.98	$w = 70.91 vol^{0.99}$	1009.05
12	6–25 mm	$\ln(w) = 5.16 + 1.98 \ln(mcw) + 3.25 \ln(h)$	0.59	0.94					

other morphometric data (Murray and Jacobson 1982, Hughes et al. 1987, Pereira et al. 1995), log-antilog transformations sometimes can result in biased estimates of biomass (Tausch and Tueller 1988). Therefore, where a logarithmic model was selected as the best model, we also present the corresponding nonlinear model, and compare the standard error of the estimate from this model with the standard error of the estimate calculated using back-transformed estimates from the logarithmic model. For these comparisons, predicted biomass from the logarithmic equation was converted to the arithmetic form (anti-log) and the standard error was computed using actual biomass and the

corresponding predicted biomass. Regressions were not performed on the component of stems > 25 mm for *L. cuneifolia*, *L. nitida*, *C. erinacea*, and *P. flexuosa* var. *depressa* because only a few individual plants of these species had large stems (n = 5, 4, 2, and 0, respectively).

For *L. divaricata*, the relationships between total biomass and relative proportions of the various components (leaves, stems < 6 mm, stems 6–25 mm, stems > 25 mm) were examined using best fit nonlinear models. The model with the highest r^2 was selected for graphical presentation.

Dry weight and volume of total aboveground biomass were used to calculate bulk density for each species. Packing

ratio, the ratio between bulk density and specific gravity (i.e., biomass per unit volume occupied by the biomass alone), is commonly used to describe the compactness of fuel (Rothermel 1972, Van Wilgen et al. 1990, Pereira et al. 1995). In fire models, specific gravity is usually considered a constant (Rothermel 1972); thus, bulk density is the primary variable that determines compactness (Brown 1981).

Results and Discussion

For all shrub species, at least 1 of the morphological measurements was a good predictor of total aboveground biomass, as

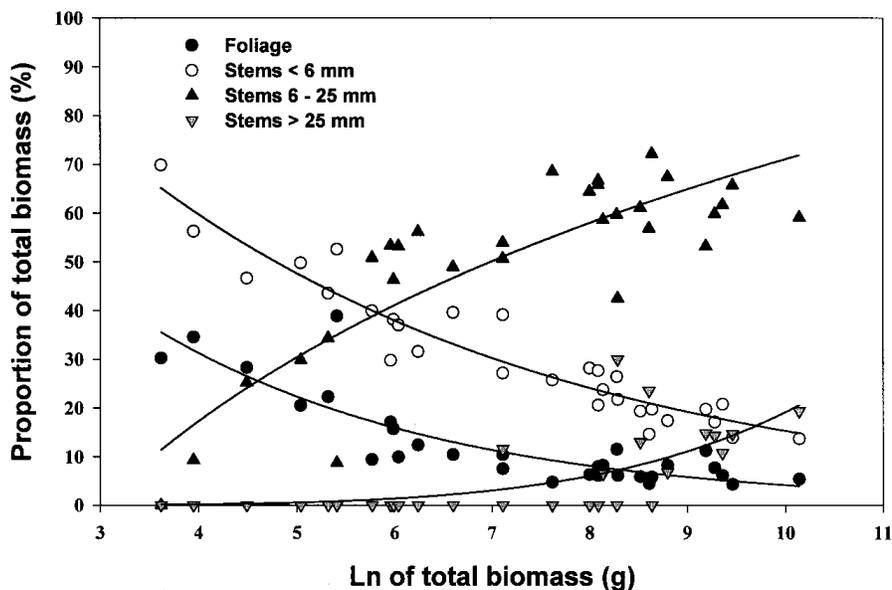


Fig. 1. Proportional biomass of foliage and stems as a function of total biomass of *L. divaricata* ($n = 30$). Foliage ($y = 120.76 e^{-0.34x}$, $r^2 = 0.75$); stems < 6 mm diameter ($y = 148.38 e^{-0.23x}$, $r^2 = 0.90$); stems 6–25 mm diameter ($y = -64.15 + 58.69 \ln(x)$, $r^2 = 0.73$); stems > 25 mm diameter ($y = 0.001 x^{5.20}$, $r^2 = 0.44$). Ln = natural log. All models are significant at $p < 0.0001$.

well as the biomass of each component (Table 2). Predictive equations developed using a single independent variable had a better fit to the data when compared to equations using 2 independent variables in all but 1 case (6–25 mm stems of *P. flexuosa* var. *depressa*). The easiest field measurement to make for 6 of the species was diameter of the longest stem, and equations for total aboveground biomass using this variable had a good fit to the data except for *C. erinacea* (Table 2).

In most cases, a natural log-log model gave the best fit between field measurements and total aboveground biomass, and between field measurements and biomass of components for linear models (Table 2), similar to results reported in other studies (Brown 1976, Ohmann et al. 1976, Murray and Jacobson 1982, Rittenhouse and Sneva 1977, Braun et al. 1979, Bryant and Kothmann 1979, Hughes et al. 1987, Pereira et al. 1995). In all species except *L. nitida*, standard errors of the estimate computed from power equations were lower than those calculated using back-transformations from log-log regression. Coefficients of determination generally were high for both log-log and power equations. In view of the potential for bias in predicting biomass from equations developed with transformed data (Sprugel 1983), power equations provide a good alternative to log-log equations for the shrub species in our study.

The plot of total aboveground biomass

vs the proportion of biomass components for *L. divaricata* (Fig. 1) indicates that as shrubs grow, the proportions of foliage and stems < 6 mm decrease, while the proportions of stems of 6–25 mm diameter and larger increase. If carbon respired by live stem tissue represents an increasingly larger amount of carbon fixed in foliage by photosynthesis, then productivity of shrubs should decrease with age. This age/productivity relationship is well known for trees in a variety of ecosystems (Ryan et al. 1997, Carey et al. 1998), but it is poorly documented for shrubs.

C. erinacea and *G. decorticans* had the highest bulk densities, *Larrea* spp., *P. caldenia*, and *C. microphylla* were intermediate, and *P. flexuosa* var. *depressa* had a much lower bulk density (Table 1). With the exception of *P. flexuosa* var. *depressa*, bulk densities of shrubs in our study area are comparable to those of shrubs in other fire-prone ecosystems (Van Wilgen et al. 1990, Pereira et al. 1995). Dead material was a small component of total aboveground biomass of the shrubs examined; the maximum mean value was 17% dead material for *P. flexuosa* var. *depressa* (Table 1). For all species, stems < 6 mm diameter represented most of the dead material [e.g., $90.8 \pm 5.4\%$ for *P. flexuosa* var. *depressa*].

As in North America, livestock ranching is the predominant land use in creosote-bushdominated ecosystems in Argentina.

Overgrazing in semi-arid ecosystems in North America has favored shrubs over herbaceous vegetation (Schlesinger et al. 1990). The impacts of livestock grazing in Argentine Monte have not been assessed, but similar patterns may occur. Fire is an important natural component of these ecosystems, and is used extensively as a management tool to control shrubs. The predictive equations for biomass developed in this study will allow rapid and accurate estimation of shrub biomass in the Monte of Argentina. This information is essential for monitoring the effects of grazing on shrub dynamics, for examining the impacts of different fire regimes on the aboveground biomass of shrubs, and for studies of ecosystem productivity.

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Technical Note: Use of digital surface model for hardwood rangeland monitoring

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Abstract

We built digital surface models (DSM) that contain 3D surface morphological information of the entire landscape using digital photogrammetry and aerial photographs. Changes in landscape components such as crown closure and tree height in hardwood rangeland were estimated using DSM. In comparison with manual interpretation results, errors of crown closure and tree height estimation using DSM were less than 0.7% and 1.5 m, respectively. This technique can be used for rangeland management, monitoring and ecological studies.

Key Words: Digital photogrammetry, photo-ecometrics, tree heights, crown closure

Hardwood rangelands cover 10% of California, and are composed of an overstory of various hardwood species, predominantly in the genus *Quercus*, and an understory mainly of introduced annuals (Griffin 1978, Bartolome 1987). Tree crown closure, also referred to as crown cover, canopy cover, and canopy closure, is defined as the percent of forest area occupied by the vertical projection of tree crowns (Avery and Burkhart 1994). It is commonly used as a measure of stand density and often used as an important indicator of wildlife habitat. Air-photo interpretation techniques have been used on these areas for hardwood classification and tree crown closure estimation. However, they are dependent on the experience of photo interpreters. Some experiments indicate that there are large discrepancies among photo interpretation results carried out by different interpreters (Biging et al. 1991, Gong and Chen 1992, Davis et al. 1995). It is difficult to develop detailed vegetation maps at the individual tree level with existing satellite imagery such as IRS, SPOT HRV and Landsat TM data because of their low spatial resolution ranging from 6 to 30 m (Congalton et al. 1991, Brockhaus and Khorram 1992, Franklin 1994). Even with high-resolution (0.5 to 2 m) multispectral videography, it is difficult to derive crown closures of conifer forest using traditional image analysis methods such as image thresholding and classification (Biging et al. 1995).

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Resumen

Mediante el uso de fotogrametría digital y fotografías aéreas construimos modelos de superficie digital (DSM) que contienen información en tercera dimensión (3D) de la superficie morfológica del paisaje completo. Con el uso de DSM se estimaron los cambios de los componentes del paisaje tales como lo cerrado de la copa y la altura de los árboles de un pastizal con árboles de madera dura. En comparación con los resultados de interpretación manual, los errores de estimación de lo cerrado de la copa y altura de los árboles con el uso de DMS fueron menos del 0.7% y 1.5 m respectivamente. Esta técnica puede ser utilizada para el manejo y monitoreo de pastizales y estudios ecológicos.

Aerial photography with conventional aerial cameras and digital cameras has some advantages over other remote sensing alternatives. First, it acquires images through a central perspective making the image geometry easier to model and hence it has better geometric precision. Secondly, it has the best spatial resolution in remote sensing, usually better than 0.1 m. Beside the wider radiometric range and high spectral resolution, the spatial resolution of digital cameras is improving rapidly. We were able to acquire aerial digital images with better than 0.2 m resolution using commercially available digital cameras. In this paper, we report some of the preliminary results obtained from applying digital photogrammetry to aerial photographs for the purpose of hardwood rangeland monitoring.

Digital Photogrammetry

Digital photogrammetry is a computerized technique that automates the measurement and mapping process of traditional photogrammetry (Saleh and Scarpace 1994). A major challenge in digital photogrammetry is image matching, a critical procedure that finds image points corresponding to the same ground point from a stereopair. Although many image matching algorithms have been developed (Ackermann 1996), this process is error-prone in forest and urban areas where abrupt vertical changes are common. We are currently working in this area to improve image matching accuracy.

The 2 primary uses of digital photogrammetry are digital elevation model (DEM) development and orthophoto generation. A

DEM of an area is usually an array of grid points of ground elevation that excludes the heights of landscape features such as trees and buildings. A digital surface model (DSM), which is an array of grid points of elevation including landscape features, is necessary for deriving tree measurements in woodland and forest settings. An orthophoto is a photo of an area with a constant scale, and free from point displacement caused by elevation differences and lens distortion. Therefore, area measurements from orthophotos are more accurate than from raw aerial photographs (Gong et al. 1999).

Figure 1 shows the results from digital photogrammetry when applied to 2 sets of scanned aerial photographs acquired in July 1970 and August 1995. The original photos were acquired with a nominal scale of 1:12,000 at the upper Gallinas Valley (38°02'38" N, 122° 36'30" W), Marin County, California. They were scanned at approximately 25m μ m from black and

white diapositives on a Vexel 3000 scanner. The digital photogrammetric software used to analyze these photos was VirtuoZo[®], a commercial software package from VirtuoZo Inc., Australia. Results shown here were generated automatically from VirtuoZo that employs the following procedures of digital photogrammetry:

- (1) internal orientation. Establishes the coordinate system for each photograph based on camera frame size, position of principal point, focal length of the camera lens and the image scanning parameters.
- (2) relative orientation. Determines the spatial position of the exposure stations and camera attitude parameters for both the left and right photos of a stereopair. This has been achieved in this study using 8 ground control points found in the photos by precisely measuring their ground coordinates at the centimeter level in the field with differential GPS equipment.

- (3) epipolar image resampling. Resamples the left and right images according to the flight line direction so that conjugate image points can be searched along a line parallel to the flight line. Thus the image matching is simplified from a 2D matching to 1D matching.
- (4) image matching. Automatically searches the conjugate image points from the left and right photos according to a similarity criterion. The absolute parallax for each image point can then be calculated. It enables the derivation of elevation for that image point. Matching algorithms are proprietary to software vendors. The precision of most matching algorithms is within one pixel. Some can reach the subpixel level. Assuming a single-pixel matching precision, the vertical resolution of the elevation data obtained here is approximately 0.5 m.

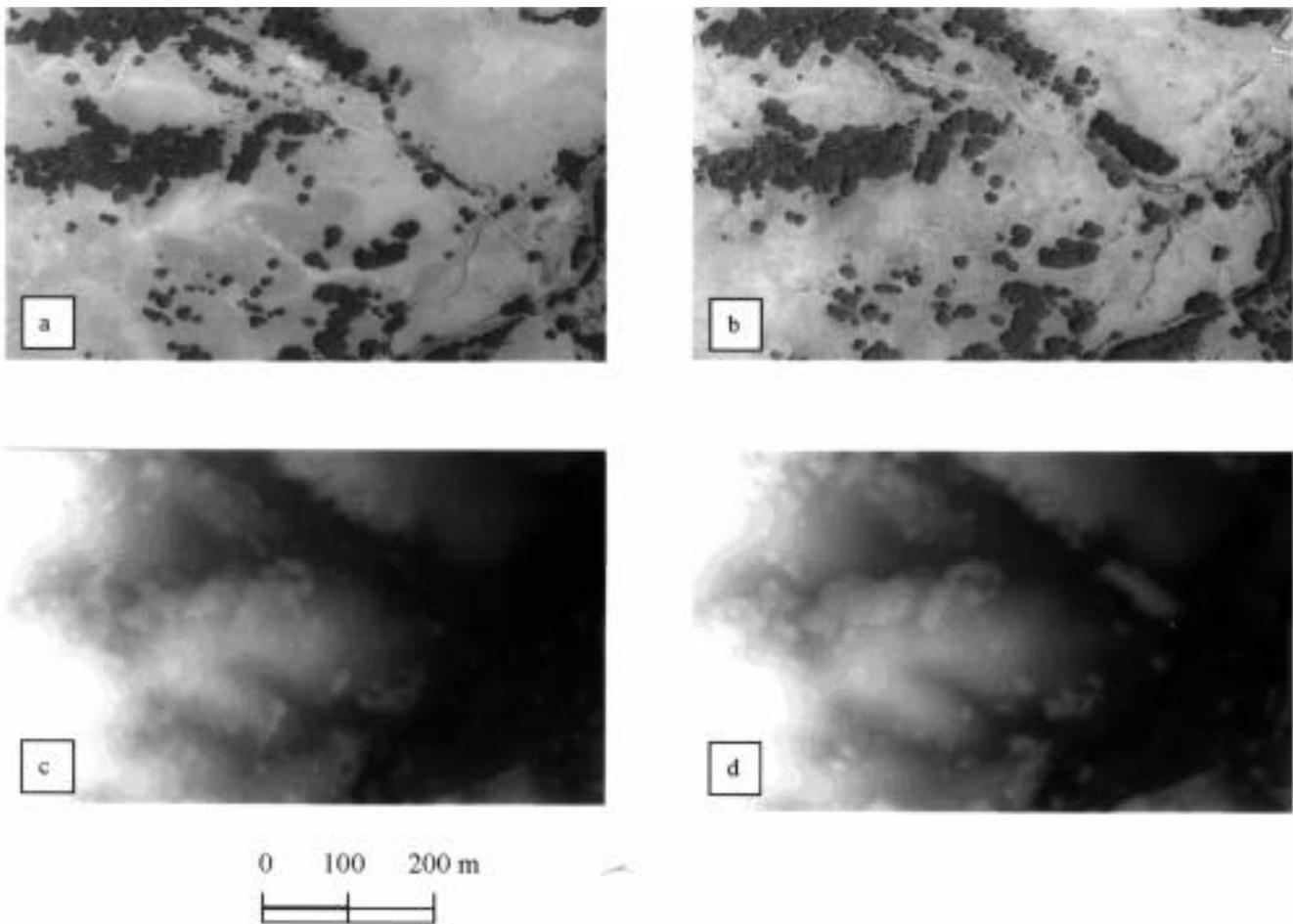


Fig. 1. Orthophotos and digital surface models (DSM) of a hardwood rangeland area in California. a. the orthophoto derived from the 1970 aerial photography, b. the orthophoto from 1995 aerial photography, c. DSM for 1970, and d. DSM for 1995. Gray scales in c and d represent surface elevation as derived from digital photogrammetry. Those mushroom-shaped bright patches in c and d are oak canopies.

- (5) absolute orientation. Determines the mathematical transformation between the image coordinate system to a geodetic coordinate system or a map coordinate system such as the Universal Transverse Mercator (UTM) system.
- (6) DSM generation. Calculates the elevation for a selected subsample of image points in a stereopair using the absolute parallax determined earlier. Due to computational complexities and difficulties in correctly matching every image point, most commercial algorithms match only a sample set of the total image points. The elevations for the rest of the image points in the image area are usually interpolated from those sample points. This smoothes elevation differences when sharp changes in elevation are encountered, causing deformation of objects with relatively steep slopes such as buildings and trees. This is a shortcoming of the existing image matching algorithms.
- (7) DEM generation. To generate a DEM, some additional algorithms are employed. These include the detection of landscape features such as buildings and trees and the removal of their heights from the DSM. Then spatial interpolation can be used to estimate the ground elevation at the locations where objects such as trees or buildings occur.
- (8) Orthophoto or contour map generation. Once the DEM or DSM is available, it can be used to rectify the perspective projection of the original raw imagery to an orthophoto with an orthographic projection. In theory, the DEM can not completely remove the image point displacement caused by object height. Such displacements can only be completely removed by an accurate DSM as it captures the elevations from both the terrain and landscape features on top of it. A contour map can be generated from either the DEM or DSM.

Hardwood Change Monitoring

Figures 1a and 1b show orthophotos for the same area from 1970 and 1995, respectively, which were generated by correcting for the scale variation in the original photographs using the 1970 and 1995 DSMs, respectively. The scanned image resolution was approximately 0.3

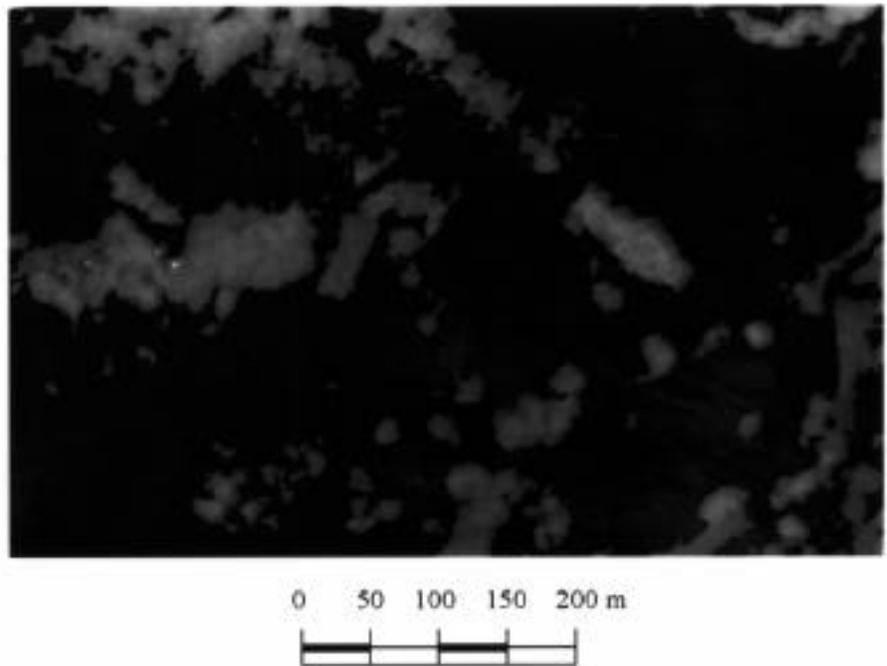


Fig. 2. The 1995 canopy morphological (height) model. This was obtained by deriving a digital elevation model (DEM) from the 1970 aerial photography then taking the difference between the 1995 DSM and the DEM. The terrain background is in black and the brightness corresponding to the height oak canopies.

m. The grid spacing used to extract the DSMs was approximately 1 m. The DSM shown in Figs 1c and 1d were interpolated to 0.3 m horizontally. The surface cover is mainly hardwood rangeland. Clusters of relatively bright areas, in Figs 1c and 1d, are coast live oaks (*Quercus agrifolia* Née). Coast live oaks can be extracted from Figs 1a and 1b through a simple image thresholding as they are radiometrically darker than their surroundings (dry grass). Changes of crown closure can be obtained by comparing the 2 thresholded images. However, this radiometric thresholding technique suffers from shadow and shading caused by the hilly topography. It is likely to produce crown closure estimates that are exaggerated. Although the shading and shadowing effects may be reduced by stratifying the study area according to the lighting conditions and by applying thresholding to each stratification, this will considerably increase the amount of work through manually partitioning the image area and editing the thresholding results. A new alternative to crown closure measurement is to threshold the heights from a crown height image derived from the DSM. This new height thresholding approach is not affected by the variation in lighting conditions but dependent on the accuracy in height determination, particularly at the edges of tree crowns whose slopes are sharp.

To evaluate the accuracy of the 2 crown closure measurement methods, we carefully digitized the oak woodland cover from a portion of the 1995 orthophoto by excluding shadows. The crown closure percentage was 26.6% (8,1962 m² tree cover divided by the total area of 30,7932 m²). The crown closure results obtained from radiometric thresholding were treated as the reference data for comparison with crown closure obtained from height thresholding. The best crown closure estimated with the radiometric thresholding method was 31.0% (95486 m² tree cover), which yielded a 4.4% overestimate of crown closure in comparison to the reference value. This overestimation was primarily caused by the difficulty in separating shadow and shade areas on the orthophoto from the tree canopies.

On the 1970 DSM, the tree crown portion can be processed by first excluding the tree crowns. After excluding the tree crowns, we can use interpolation to estimate the ground surface elevation in the areas occupied by tree crowns. Although the interpolation can be done in commercial GIS software packages such as terrain analysis modules in the ESRI Arc/Info, we did it by manual editing on the computer screen. This process gives us a DEM. Assuming that the topography does not change in this area, we subtracted the DEM from the 1995 DSM to produce a

crown height image (Fig. 2). Tree heights and crown closure can be measured from this image. Experimenting with a few height thresholds, we obtained the best results with a threshold of 2 m. The crown closure estimate was 27.3% (84,173 m² tree cover), only 0.7% overestimate of crown closure in comparison to the reference data. We applied this methodology to both the 1970 and 1995 crown height images to determine the changes in crown closure. There was an overall net change of approximately +1.4% in crown closure over our study area during this 25-year period. However, this number is comprised of 3 components—increase in canopy closure due to growth in existing tree crown dimensions, increase due to recruitment of new trees (regeneration) and decrease due to tree mortality. There was approximately a 5.0% decline (relative to 1970) in crown closure due to tree mortality. The surviving trees accounting for a growth in crown closure of approximately 6.4%.

The brightest spots on each tree crown in Fig. 2 represent the highest point on the canopy. We arbitrarily selected 29 locations on different tree canopies in the image area and obtained their heights using both manual and automatic methods. The manual method was based on the image point matching through stereoscopic viewing of the stereo pair on the computer screen. This method was used as reference for accuracy evaluation because field measurement is not possible at present. Visual image matching was done in non-digital photogrammetry as a standard approach for height determination. The automatic method was based on the direct reading of the elevation data determined through the image matching algorithm. We did not measure the height at the tallest position of each tree canopy in order to assess the capability of the computer algorithm for height measurement at all possible canopy positions. Since both the 1995 and 1970 elevation data were transformed into the same UTM coordinate system, the distribution of the 29 canopy positions in the horizontal plane was kept the same for both the 1970 and 1995 data. This allows us to determine the canopy growth during the past 25 years. Table 1 shows a comparison of tree heights obtained with the 2 methods. While the absolute differences between the 2 methods can be greater than 4 m, the average differences were 1.50 m and 1.21 m for the 1970 and 1995 photos, respectively. Treating the results obtained with the manual method as accurate, the stan-

Table 1. Heights automatically measured from different positions of tree canopies in comparison with the corresponding heights determined by manual photogrammetric method.

Canopy position ID	1970			1995		
	Manual	Automatic	Abs. Error	Manual	Automatic	Abs. Error
1	9.50	9.03	0.47	10.28	8.76	1.52
2	2.33	3.91	1.57	7.92	5.19	2.73
3	10.84	7.95	2.89	9.27	8.49	0.78
4	7.09	11.73	4.64	14.69	13.07	1.62
5	8.18	8.11	0.07	9.11	9.70	0.59
6	3.20	3.98	0.78	6.32	8.17	1.85
7	7.57	7.48	0.09	7.77	8.39	0.62
8	4.99	3.20	1.79	6.55	6.28	0.27
9	9.10	7.17	1.92	9.31	8.41	0.90
10	7.33	5.54	1.78	6.62	6.79	0.17
11	4.22	1.39	2.83	3.61	3.79	0.18
12	1.78	4.22	2.44	6.61	6.00	0.60
13	7.27	5.79	1.48	6.78	6.49	0.29
14	3.07	1.19	1.88	4.66	4.14	0.52
15	7.58	6.93	0.64	2.53	5.73	3.20
16	7.45	7.07	0.38	7.65	5.85	1.81
17	2.52	3.11	0.59	4.40	7.18	2.78
18	0.80	4.76	3.96	9.88	8.38	1.50
19	5.38	5.07	0.31	6.55	2.26	4.29
20	2.61	3.64	1.03	6.28	6.71	0.43
21	4.47	4.41	0.06	13.15	12.50	0.65
22	3.12	5.92	2.80	6.61	7.72	1.12
23	8.53	7.86	0.67	7.43	6.35	1.08
24	1.00	3.28	2.28	3.26	4.40	1.13
25	2.79	2.51	0.28	3.18	3.76	0.58
26	4.50	2.47	2.02	3.32	4.02	0.70
27	6.85	8.76	1.91	10.71	10.47	0.24
28	7.64	5.86	1.78	1.65	4.44	2.78
29	6.25	6.34	0.09	6.69	6.56	0.13
Average	5.45	5.47	1.50 (1.94) ¹	6.99	6.90	1.21 (1.64)

¹Numbers in brackets are standard deviations.

dard deviations were 1.94 m and 1.62 m for the 1970 and 1995 photos, respectively. Considering the relatively small photo scale, an error level of less than 2 m is quite reasonable. The averages of tree canopy heights for each year were very close (within 10 cm) between the 2 height measurement methods. The average growth of canopy height, derived from the averages in Table 1, was 1.54 m for the manual method and 1.43 m for the automatic method.

Discussions and Conclusion

Our preliminary results demonstrate the advantage of DSMs for tree height and crown closure measurement because they are not affected by crown shadow and shading caused by topographic relief. When canopy cover is relatively sparse as in this study, the ground elevation for a relatively large portion of the imaged area can be directly measured by the digital photogrammetric method. In this situation the accuracy of the entire DEM can be relatively high because we only need to inter-

polate over a small fraction of the landscape where scene objects such as trees obscure our direct observation of the ground. This in turn leads to a relatively high accuracy in the crown height image. However, the accuracy of a DEM determined with photogrammetric methods usually decreases as the total crown closure increases. Thus in dense hardwood stands the crown height image will be less accurate in making tree height measurements than more open stands. Nevertheless, the accuracy in estimating the change in height of trees is not affected by changes in tree crown closure because the DSMs are accurate even when the DEMs are not. In addition, the 3D crown shapes obtained from a DSM contain crown structure information that should be useful in automated tree species recognition. Some of the mathematical morphology techniques hold strong promises for application to forest type recognition (Zheng et al. 1995).

The current situation is that stereo photography lacks spectral depth, but allows for precise spatial measurements. The current generation of satellite images have more and narrower spectral bands than

photographs, but are not of high spatial resolution and high geometric precision. Digital cameras bridge this gulf by providing imagery which is of both high spatial (better than 0.5 m) and spectral resolution (20 to 50 nm) with a sufficient number of spectral bands. This will enable us to develop new computational algorithms for image processing and digital photogrammetry to extract the maximum amount of information contained in aerial photographic images and to provide the parameters needed for land resource management, monitoring and ecological studies. This can provide useful approaches to evaluating changes in habitat value, rangeland carrying capacity, and tree mortality and recruitment trends.

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Protocol for monitoring standing crop in grasslands using visual obstruction

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Abstract

Assessment of standing crop on grasslands using a visual obstruction technique provides valuable information to help plan livestock grazing management and indicate the status of wildlife habitat. The objectives of this study were to: (1) develop a simple regression model using easily measured visual obstruction to estimate standing crop on sandy lowland range sites in the Nebraska Sandhills, (2) provide sampling and monitoring suggestions in the use of visual obstruction on this grassland type, and (3) compare the visual obstruction technique to the standard clip and weigh procedure. Visual obstruction precisely predicted average standing crop dry weights for the sandy lowland range sites ($r^2 = 0.88$). A prediction accuracy of $\pm 295 \text{ kg ha}^{-1}$ was found using a test data set. Two sampling options (A and B) were evaluated using a 2-stage sampling protocol. Option A (1 transect/quarter section) provided more precise estimates applicable to extensive grasslands than option B. However, option A was not applicable to a section (259 ha) or a few sections. Option B (3 transects/section) provided estimates applicable to each section and to the entire area, but it required more intensive sampling than option A to attain the same precision. The visual obstruction technique provided more precise estimates of standing crop than the standard clip and weigh technique when clipping and weighing up to 6 plots per transect. When 7 or more clipped and weighed plots per transect were sampled, standing crop estimates were more precise than using visual obstruction readings. However, since 20 visual obstruction readings/transect (25 minutes) can be sampled in about half the time spent clipping and weighing 6 plots/transect (45 minutes), visual obstruction in combination with a previously estimated regression model provides a simple, reliable, and cost effective alternative to the clip and weigh technique. Regression models should be developed for other grassland types following the methodology described in this paper.

Key Words: Residual cover, grassland structure, regression model, wildlife habitat, Robel pole, Nebraska Sandhills

Herbage standing crop on grasslands is valued for multiple uses such as livestock production, wildlife food and cover, and soil protection against erosion. Assessment of grassland standing crop using a visual obstruction technique provides important informa-

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Resumen

La evaluación del forraje en pie del pastizal utilizando la técnica de obstrucción visual provee valiosa información que ayuda a planear el manejo del apacentamiento del ganado e indicar el estado del hábitat de la fauna silvestre. Los objetivos de este estudio fueron: (1) desarrollar un modelo de regresión simple utilizando la obstrucción visual simple (que es fácil de medir) para estimar el forraje en pie en sitios de pastizal de tierras bajas arenosas en los pastizales "Nebraska "Sandhills", (2) proveer sugerencias sobre el muestreo y monitoreo con el uso de la técnica de obstrucción visual en este tipo de pastizales y (3) comparar la técnica de obstrucción visual con la técnica de cortar y pesar. La obstrucción visual predijo en forma precisa el promedio de peso seco de la producción de forraje en pie de los sitios de pastizal de tierra baja arenosa ($r^2 = 0.88$). Con el conjunto de datos experimentales utilizados se encontró una certeza de predicción de $\pm 295 \text{ kg ha}^{-1}$. Se evaluaron dos opciones de muestreo utilizando un protocolo de muestreo de dos etapas. La opción A (1 transecto/cuarto de sección) produjo estimaciones más precisas aplicables a pastizales extensivos que las estimaciones obtenidas con la opción B. Sin embargo, la opción A a no fue aplicable a una sección (259 ha) o a unas pocas secciones. La opción B (3 transectos/sección) rindió estimaciones aplicables a cada sección y el área entera, pero requirió un muestreo más intensivo que la opción A para obtener la misma precisión. La técnica de obstrucción visual produce estimaciones más precisas del forraje en pie que la técnica de corte y peso cuando se cortan y se pesan hasta 6 cuadrantes por transecto. Cuando se cortan y pesan 7 o más cuadrantes por transecto las estimaciones del forraje en pie fueron más precisas que las obtenidas con la obstrucción visual. Sin embargo, dado que 20 lecturas/transecto de la técnica de obstrucción visual (25 minutos) pueden ser obtenidas en casi la mitad del tiempo utilizado para cortar y pesar 6 cuadrante/transecto (45 minutos), la obstrucción visual en combinación con un modelo de regresión previamente estimado provee un alternativa más simple, confiable y menos costosa que la técnica de corte y peso. Los modelos de regresión deben ser desarrollados para otros tipos de pastizales siguiendo la metodología descrita en este artículo.

tion to plan livestock grazing management and to evaluate habitat conditions for various grassland wildlife species (Webb 1942, Slade et al. 1965, Higgins and Barker 1982, Higgins 1986).

For decades, a common method to obtain standing crop dry weight estimates has been the double sampling method (Pechanec and Pickford 1937). This method consists of visually estimating

herbage weight for a large number of plots. A portion of these plots are visually estimated and the herbage is clipped. The clipped herbage is oven dried and weighed. Oven dried weights are then used to correct visual estimates through a regression model. This technique can be costly and time consuming as large sample sizes may be required to produce precise estimates.

Several non-destructive techniques, such as the biometer (Pearson and Miller 1972), the Massey grass meter (Holmes 1974), the Ellinbank pasture meter (Earle and McGowan 1979), and the rising plate meter (Michell and Large 1983, Gabriëls and Van Den Berg 1993), have provided estimates of standing crop with high degrees of accuracy. However, they were not designed to measure vegetation visual obstruction, a height-density measurement that relates to values of the environment in which wildlife live (Webb 1942, Robel et al. 1970, Higgins and Barker 1982, Higgins 1986).

Visual obstruction can be used to estimate the amount of standing crop dry weight as an alternative to clipped plots to minimize cost and effort for monitoring grasslands. Standing crop dry weight estimates can be indirectly obtained using easily measured visual obstruction (Robel et al. 1970) in regression models. The status of wildlife habitat can be quantified using visual obstruction as an estimate of vegetation height-density (Webb 1942, Robel 1966, Higgins and Barker 1982, Higgins 1986).

The rationale for using visual obstruction to monitor standing crop and vegetation height-density on grasslands is based on the simplicity of this technique, dual measurements obtained from each use of the pole (vegetation dry weight for livestock production and height-density for wildlife habitat status), and application over broad areas with less effort (no clipping and bagging and no drying and weighing) than the standard clip and weigh procedures. Our purpose was to develop simple regression models to use easily measured visual obstruction to accurately predict average amounts of standing crop for livestock management and simultaneously determine the status of grasslands for wildlife habitat. The objectives were: (1) to develop and test models used to estimate grassland standing crop using a graduated pole, (2) compare the time spent (cost) and efficiency of the visual obstruction technique versus the clip and weigh technique, and (3) determine sampling intensities and monitoring

guidelines needed to use visual obstruction on grasslands for standing crop dry weight and vegetation height-density assessments.

Materials and Methods

Study Area

This study was conducted on the Samuel R. McKelvie National Forest (SMNF) located 43 km southwest of Valentine, Nebraska (42°N, 101°W). This area includes sand dune hills, sandy basins, and valleys that are stabilized by vegetation (Bleed and Flowerday 1990). The study, however, focused on the vegetation in the sandy lowland range sites where native graminoids dominate. Little bluestem (*Schizachyrium scoparium* Michx.), prairie sand reed (*Calamovilfa longifolia* Hook.), and needle-and-thread (*Stipa comata* Trin. & Rupr.) are the dominant species. Other common species include sun sedge (*Carex* spp. Mack.), sand bluestem (*Andropogon hallii* Hack.), hairy grama (*Bouteloua hirsuta* Lag.), blue grama (*Bouteloua gracilis* H.B.K.), switchgrass (*Panicum virgatum* L.), Kentucky bluegrass (*Poa pratensis* L.), sand lovegrass (*Eragrostis trichodes* Nutt.), sand dropseed (*Sporobolus cryptandrus* Torr.), and common ragweed (*Ambrosia artemisiifolia* L.). Soils belong to the Ipaga and Inavale loamy fine sand series with 0 to 3% slopes (USDA-SCS 1993). Elevations range from 1,219 to 1,310 m above sea level, rising gradually from east to west. Average annual precipitation is 436 mm, most of it falling from April to September. Precipitation from October to March falls as snow. The mean annual temperature is 8.3°C. Average maximum temperature is 16°C and average minimum temperature is 1°C. The average frost-free period is 150 days (National Climate Data Center 1993).

Data Collection and Analyses

Visual obstruction and clipped vegetation data were collected in the fall of 1996 after a killing frost. A modification of the pole described by Robel et al. (1970) was used to measure visual obstruction and a 0.25 m² circular quadrat was used to clip and harvest vegetation. The width of alternating grey and white bands on the pole was modified from 1 dm to 2.54 cm wide. The bands were numbered beginning with 1 at the bottom. The bottom of the pole had a 15 cm spike which allowed it to stand free once the spike was pushed into the ground. The graduated pole was placed in the center of the circular quadrat and

visual obstruction readings (VORs) were made from a distance of 4 m with the reader's eyes at a height of 1 m (Robel et al. 1970). The top band totally obstructed was recorded as a reading. If the first band was visible, the reading was zero. A reading of 1 meant that the first band was totally obstructed by vegetation. At each measurement station, 4 VORs were recorded, 1 for each cardinal direction. The 4 VORs were averaged for each station and multiplied by 2.54 to convert to centimeters.

A stratified sampling design (Cochran 1977, Cook and Stubbendieck 1986) was used to collect vegetation (live and dead) data. Strata were structured so that an equal number of pastures representing tall to very short vegetation were sampled to provide a broad range of data to estimate the regression relationship. The sampling design included 58 pastures (300 to 550 ha each) with 3 randomly located transects per pasture. Along each 200 m transect, 20 pole stations spaced 10 m apart were read for visual obstruction and 4 stations were clipped (50, 100, 150, and 200 m) for standing crop estimates. Vegetation within the circular quadrat was clipped at ground level, oven dried at 60°C for 48 hours, and weighed to the nearest gram. Standing crop was expressed in kg ha⁻¹.

Regression was used to quantify the relationship between visual obstruction and standing crop. The average of the VORs for each transect was the independent variable and the average of the 4 standing crop estimates was the dependent variable. Probability plots were used to examine normality of residuals (Kleinbaum and Kupper 1978, Afifi and Clark 1990). Prediction accuracy of the developed regression model was checked at the 0.05 level of significance using methods outlined by Freese (1960) for a separate data set (average dry weight = 913 kg ha⁻¹ with SE = 104, average VOR = 4.82 cm with SE = 0.62, and n = 19 transects) that was collected in the fall of 1996. The transects were randomly located within 19 pastures (1 transect/pasture).

Sampling Intensity

Estimation of sample size for future applications of visual obstruction was based on within and between transect variability in the grassland. The average visual obstruction for each transect was obtained from reading 20 stations. The number of transects needed to achieve estimates within ± 20% of the actual mean with an 80% confidence interval was estimated for each pasture. A box-and-whisker plot

(Chambers et al. 1983) was used to display the required number of transects. The required number of sampling stations per transect was estimated using a reading precision of half a band (1.27 cm) on the graduated pole with an 80% confidence level. Cochran's (1977) method for sample size estimation for continuous data was used for both analyses. A Box-Ljung test (Cryer 1986) was used to assess the significance of serial correlation among consecutive sampling stations to estimate the minimum recommended interval between stations along a transect. Variance component estimation (SAS Institute 1989) was used to compare the variability among reading directions per station to the variability among stations per transect to determine whether multiple readings per station were required.

Sampling Alternatives

The size of area (percentage of total land base) to be sampled to monitor the grassland with the pole was estimated by

$$n = \left(\frac{tS}{E}\right)^2 / \left(1 + \left(\frac{1}{N} \left(\frac{tS}{E}\right)^2\right)\right)$$

(Cochran 1977), where n is the estimated number of management units to be sampled (a management unit was approximately equal to a section, 259 ha), N is the total number of management units to be monitored, S is the estimated variance among management unit means, t is the value for the t-distribution with $n-1$ degrees of freedom and 80% confidence, and E is the specified fixed error around the mean. The percentage of total land base is derived from the ratio n/N .

The percentage of total land base corresponds to the number (n) of primary sampling units. In this case, n refers to the number of sections that would be randomly selected for sampling. Based on the variability of visual obstruction on grasslands in the National Forest (SMNF), we propose 2 options for a 2-stage cluster sampling protocol, with either a quarter section as a primary sampling unit where 1 transect is used as a single subunit (option A, low sampling intensity for large areas) or a whole section (option B, high intensity sampling for a pasture or a few pastures) as a primary sampling unit where 3 transects are used as subunits. The number (N) of primary units for a total land base is fixed (e.g. 181 sections or 724 quarter sections for the SMNF) and the number of possible subunits (M) within each primary unit is assumed to be large (i.e. possible transect locations within a quarter section or a section are numerous). In 2-stage cluster sampling, the first stage is a ran-

dom draw of primary units (sections) followed by a second stage random draw of subunits (transects) within each selected primary unit. Estimation of overall mean and variances is presented below for quantitative parameters (e.g. mean visual obstruction) and proportion of residual vegetation (e.g. proportion with VOR < 7.5 cm). Notation for overall mean and variance is N primary units, each with M subunits. A sample of n primary units is randomly drawn; m subunits are randomly selected within each primary unit. Let y_{ij} be the sampled visual obstruction for the j -th subunit in the i -th primary unit (e.g. VOR for the j -th transect in the i -th pasture). Estimators are developed from:

$$\bar{y}_i = \sum_{j=1}^m \frac{y_{ij}}{m}, \quad \bar{y} = \sum_{i=1}^n \frac{\bar{y}_i}{n},$$

$$s_1^2 = \frac{\sum_{i=1}^n (\bar{y}_i - \bar{y})^2}{n-1}, \quad s_2^2 = \frac{\sum_{i=1}^n \sum_{j=1}^m (y_{ij} - \bar{y}_i)^2}{n(m-1)}.$$

\bar{y} is the estimate of overall mean VOR. The variance of \bar{y} is estimated by:

$$v(\bar{y}) = \frac{1-f_1}{n} s_1^2 + \frac{f_1(1-f_2)}{mn} s_2^2,$$

$$\text{where } f_1 = \frac{n}{m} \text{ and } f_2 = \frac{m}{M}$$

M is assumed to be quite large relative to m , such that $f_2 \rightarrow 0$. Notation for a proportion in a class (e.g. VOR < 7.5 cm) is similar except the basic observation is p_i , the proportion of m subunits falling in a class for the i -th primary unit. Also,

$$\bar{p} = \sum_{i=1}^n \frac{p_i}{n}, \quad s_1^2 = \frac{\sum_{i=1}^n (p_i - \bar{p})^2}{n-1},$$

$$s_2^2 = \frac{m}{n(m-1)} \sum_{i=1}^n p_i q_i, \text{ where } q_i = 1 - p_i.$$

Variance of \bar{p} is estimated by:

$$v(\bar{p}) = \frac{1-f_1}{n(n-1)} \sum_{i=1}^n (p_i - \bar{p})^2 + \frac{f_1(1-f_2)}{n^2(m-1)} \sum_{i=1}^n p_i q_i.$$

Time Allocation

The amount of time spent collecting visual obstruction data averaged 1 min 15 sec per station. For the clip and weigh technique, 1 min 15 sec per station was spent in labeling bags (date, area, allotment, pasture, transect, and station), 5 min 17 sec in harvesting vegetation, and 46 sec

for laboratory work (drying, weighing and recording weights, and storing samples) for a total of 7 min 28 sec per sample.

Results

Regression

The relationship between standing crop and visual obstruction was strongly linear as indicated by the high coefficient of determination ($r^2 = 0.88$, Fig. 1). Examination of probability plots indicated residuals were normally distributed. The regression model predicted the test data with an average error of $\pm 295 \text{ kg ha}^{-1}$ at a 95% level of confidence. However, prediction of single values of standing crop will have a greater relative error (%) with small Visual Obstruction Readings (VORs), but this decreases substantially for larger VORs (Fig. 2). For an estimate of $3,000 \text{ kg ha}^{-1}$, the relative error would be about 10% which corresponds to an absolute error of 300 kg ha^{-1} . In contrast, for an estimate of 600 kg ha^{-1} , the relative error would be about 50% which corresponds to an absolute error of 300 kg ha^{-1} . The relative error in estimated standing crop increases substantially for smaller VORs but the absolute error is constant at 300 kg ha^{-1} throughout the range of prediction.

Sampling Intensity

The estimated number of transects needed in each pasture to attain estimates within $\pm 20\%$ of the mean with an 80% confidence interval are displayed in Figure 3. Three transects per pasture would attain the precision objective on more than 90% of the 58 sampled pastures. The number of stations per transect needed to attain an estimate within \pm half a band (1.27 cm) on the graduated pole with an 80% confidence interval can be obtained using Figure 4. Once a preliminary estimate of vegetation visual obstruction is obtained for the entire area to be sampled, the number of sampling stations per transect can be read by matching the number of stations with the estimated VOR. A more conservative approach would be to estimate the number of sampling stations based on the transect average of highest VORs contained in the area. For the entire national forest (SMNF), the average of high VORs was about 10 cm which matched with 20 stations per transect (Fig. 4). Serial correlations among consecutive sampling stations along a transect indicated that a 10 m interval was long enough for observations to be uncorrelated ($p > 0.05$) for about 90% of the transects for

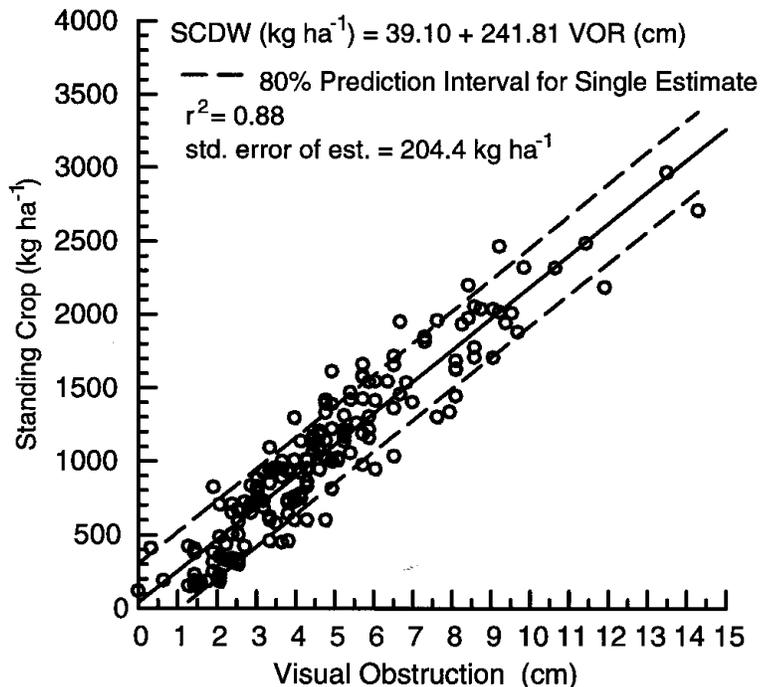


Fig. 1. Scatter plot of standing crop (kg ha⁻¹) on a dry weight (SCDW) versus visual obstruction readings (cm) with associated regression model and 80% prediction intervals for a single estimate.

the first three intervals (10, 20, and 30 m between stations) under a null hypothesis of random pattern. Variance component analysis showed that 89% of the transects required 4 readings at each station to produce reliable VORs.

Sampling Alternatives

Estimated fractions of total land base that need to be sampled to attain a precision on mean VOR of ± 1.27 cm with an 80% confidence level are displayed in Figure 5. Because the magnitude of change in the iterative estimates of sampling fractions were getting substantially smaller after 10%, the inflection point, a sampling fraction of 10% or higher is recommended for areas 15,000 ha and larger.

For the compared options (A and B) within a 2-stage cluster sampling protocol, mean VOR was $\bar{y} = 4.74$; $s_1^2 = 5.23$; $s_2^2 = 1.95$, where s_1^2 was the variance among primary units and s_2^2 the variance among subunits. This assumed pastures were the primary sampling units ($n = 58$) and transects the subunits ($m = 3$). There are 46,929 ha on the SMNF. Assuming a pasture approximately equals a section (259 ha), then $N = 181$ sections, or

$$f_1 = \frac{n}{N} = \frac{58}{181} = 0.32,$$

and $v(\bar{y}) = 0.0613(94.46\%) + 0.0036(5.54\%) = 0.065$, or a standard error of 0.25. The percentages indicate the

amount of total variance associated with primary and subunits. For the SMNF, the variance was almost totally from variation among primary units, apparently because of relatively homogeneous visual obstruction within pastures. The average proportion of transects representing residual vegetation (on grazed area) with VOR < 7.5

cm was $p = 0.69$, with variance $v(\bar{p}) = 0.00083(83\%) + 0.00017(16\%) = 0.001$ or a standard error of 0.032.

Assuming that variability among and within primary sampling units is comparable to the variability observed using SMNF 1996 data, alternative sampling plans can be evaluated by specifying appropriate N , n , and m . Different levels of variability could also be specified if appropriate (and known). For example, applying option A (1 transect/quarter section) to the SMNF would mean $N = 724$, $n = 72$ (10% sample), $m = 1$ (treating quarter sections as primary units and transects as single subunits), $s_1^2 = 5.23$ and $v(\bar{y}) = 0.0654$. Estimation of a proportion for $m = 1$ would use simple random sampling methodology resulting in $v(\bar{p}) = 0.03$. Applying option B (3 transects/section), $N = 181$, $n = 18$ (10% sample), $m = 3$ (treating sections as primary units and transects as single subunits), $v(\bar{y}) = 0.261 + 0.003 = 0.264$, and $v(\bar{p}) = 0.11$. Option A (using 10% out of 724 quarter sections) allowed the target N (the number of primary sampling units) to increase 4 times (1 section = 4 quarter sections) which required that 72 randomly located transects be sampled throughout the total land base. Option B (using 10% out of 181 sections) resulted in the requirement that 18 sections, as randomly located primary units, be sampled throughout the total land base with 3 transects per section as subunits. Option A produced a more precise overall estimate of average visual obstruction and overall (not

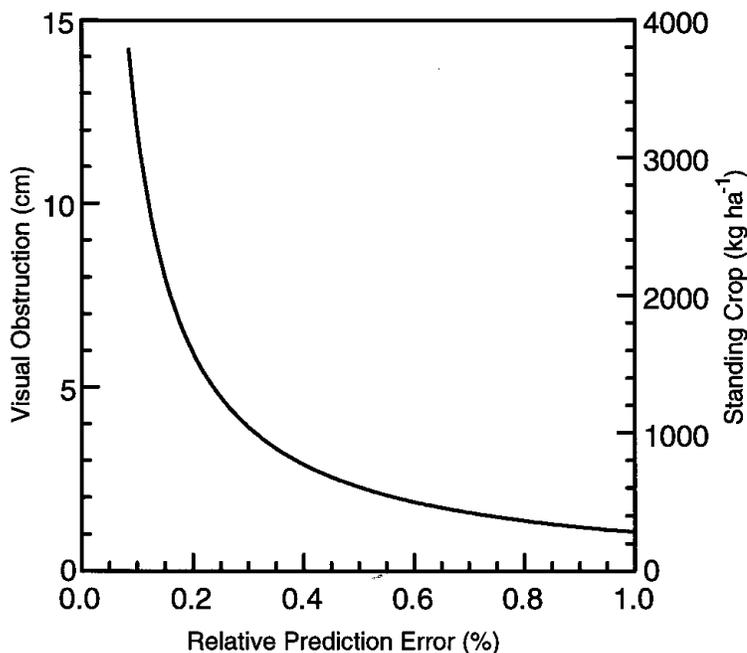


Fig. 2. Estimated prediction error associated with visual obstruction readings and predicted standing crop.

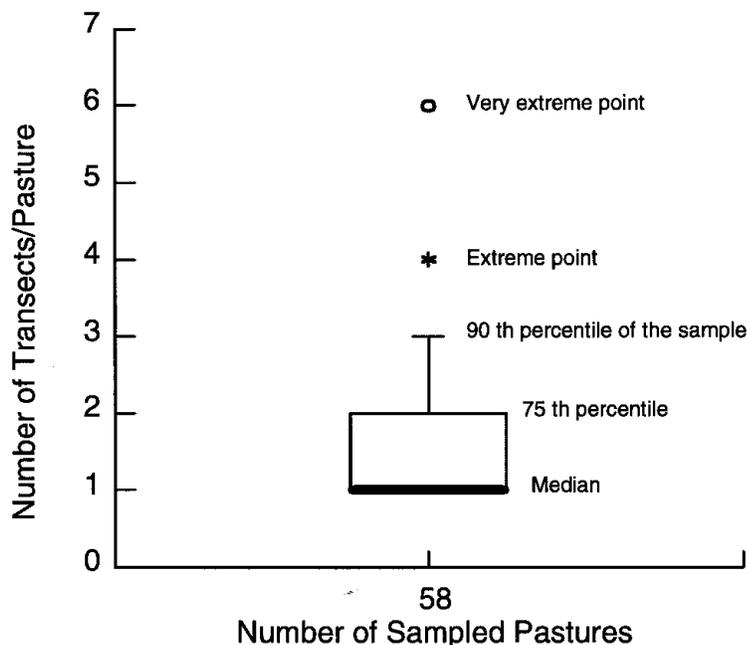


Fig. 3. Estimated number of transects per section for 58 sampled pastures required to attain a precision of $\pm 20\%$ of the mean VOR with an 80% confidence level. The median required sample size was one which extended over 50% of the sampled area. However, 3 transects per pasture or section were adequate for 95% of the sampled area.

average) p applicable to the entire area, but not applicable to a section (259 ha) or a few sections. Option B provided estimates applicable to each section and to the entire area (46,929 ha), but it would require more

intensive sampling than option A to attain the same level of precision.

Time Allocation

The recorded time ratio (visual obser-

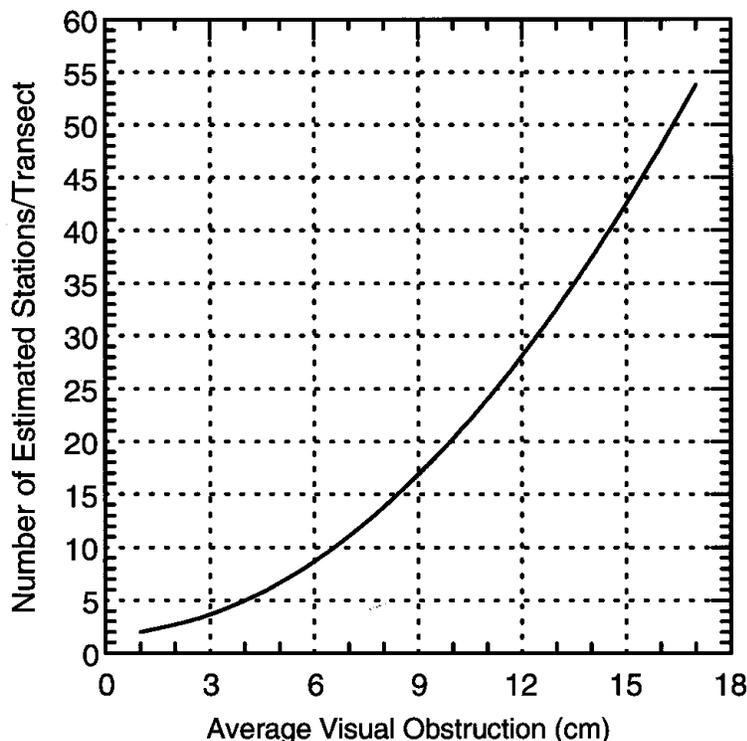


Fig. 4. Number of sampling stations for an individual transect to attain a reading precision of \pm half a band (1.27 cm) on the graduated pole with an 80% confidence level.

tion versus clip and weigh technique) was evaluated at 1 min 15 sec: 7 min 28 sec. To compare the 2 field sampling techniques in a framework in which only 1 technique would be used, we assumed that visual obstruction would be used in a previously-determined regression model to estimate standing crop for each transect. This allowed estimation of comparable standard errors. The effect of using a Visual Obstruction Reading (VOR) in a regression model to estimate standing crop was evaluated in a measurement error model (Fuller 1987) that included a component for the variability in the regression model relating visual obstruction and standing crop, a component for the variability in VORs taken along a transect, and a component for the variability in clipped and weighed standing crop. For 6 or fewer clipped and weighed plots per transect, visual obstruction estimates were more precise for our data (Fig. 6). For 7 or more clipped and weighed plots per transect, clipped and weighed estimates were more precise, regardless of the number of visual obstruction stations sampled.

Discussion

Regression results showed that visual obstruction was highly related to standing crop. Prediction of average standing crop was made with high accuracy and precision. However, the relative error of prediction was large for small Visual Obstruction Readings (VORs), while the absolute error remained constant throughout the range of prediction at 300 kg ha^{-1} . Therefore, the lowest prediction of standing crop to be considered for management purposes should be limited to 300 kg ha^{-1} . Furthermore, pastures in the Sandhills area, with standing crop equal to or less than 300 kg ha^{-1} (which correspond to a VOR of about 1.3 cm), visually show little vegetation to require a measurement technique to decide management alternatives. Strong correlation between visual obstruction and vegetation weight was also obtained in a Kansas grassland by Robel et al. (1970) using a pole with alternating light-brown and white 1 dm wide bands.

Interpretation of our data indicated that the visual obstruction technique was faster and more precise than the clip/weigh procedure when clipping and weighing 6 or fewer plots per transect. Less time was spent sampling 20 visual obstruction stations (25 minutes) compared to hand harvesting and processing 6 clipped plots (45 minutes) to obtain equal precision. With

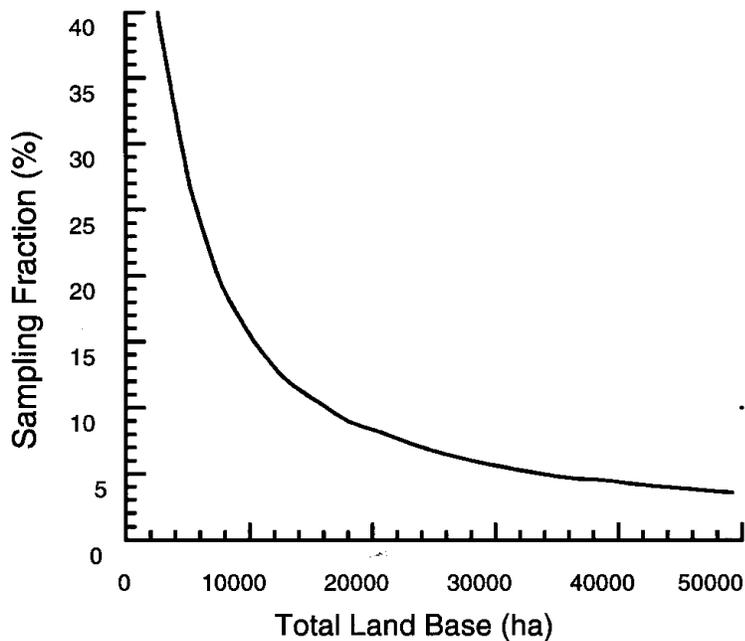


Fig. 5. Estimated percentage of total land base that should be sampled when applying the visual obstruction pole to large areas for monitoring purposes. The area to be sampled was divided into sections (259 ha). Each section was subdivided into quarter sections with one section randomly selected for placement of one transect.

the visual obstruction technique less time was spent obtaining a visual obstruction estimate per transect; thus, the visual obstruction technique can be more economical to use when monitoring large

grassland areas for average standing crop. Assessment of monitoring alternatives, using a minimum of 10% of total land base for sampling broad grasslands, showed that with option A, the number of

primary units increased to 72 which resulted in more sections included and better distribution throughout the entire land base. With option B, fewer primary units (18) were needed to sample the entire land base but more sampling subunits (3 transects) per section and resulted in better distribution within a section. Option A did not provide reliable estimates of visual obstruction or standing crop for a section or a few sections but it required lower sampling intensity than option B, thus was less costly when estimating an average visual obstruction for a large area (e.g., SMNF 46,929 ha). Option B required more intensive sampling than option A, so was more costly when dealing with a broad area but was capable of providing reliable estimates (standard error for individual section averaged 0.81 or ± 1.33 with 80% confidence) of visual obstruction and standing crop for both an individual section or an entire land base. Increasing n would increase the comparability of options A and B for describing the entire area while maintaining precision of estimates for individual units (80% confidence interval of ± 1.27 cm on average for our data).

Application

Visual obstruction (VOR) sampling can be conducted by 1 person following the procedure described by Robel et al. (1970). The pole (grey and white bands) should be placed vertically in the vegetation at arm's length to avoid trampling effects on the vegetation or biased sampling, and then spiked into the ground to stand freely. The top band totally obstructed is read and the measurement recorded. Visual obstruction readings are collected at stations along transects. The 4 VORs recorded for each cardinal direction are averaged for each station and then all stations are averaged for each transect. Transect averages are then applied separately in the regression model to obtain standing crop estimates. These same transect averages for visual obstruction can be used to estimate average amounts of residual material for wildlife nesting and thermal cover. For areas larger than 1,000 ha, we recommend option A where the transect estimate represents the section estimate. For small areas (one or a few sections), we recommend Option B where the section estimate should be the average of 3 transect estimates. For large areas, Figure 5 should be used to determine the percentage of total area (ha) to be sampled.

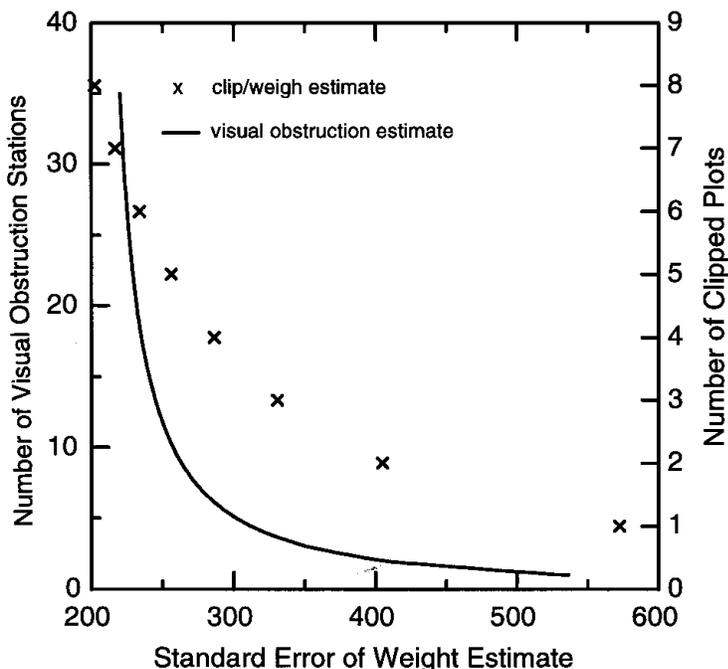


Fig. 6. Comparison of precision for weight estimates based on clip/weigh direct estimates and visual obstruction pole indirect estimates using a regression model.

Conclusions

The developed protocol should be used to adapt the visual obstruction technique for monitoring standing crop of extensive grassland areas. The regression equation described in this study is applicable to sandy lowland range sites of the Nebraska Sandhills. Other regression equations should be developed for other grassland types following the methodology developed in this paper. The visual obstruction technique is simple, cost effective, and provides dual information pertinent to livestock and wildlife management.

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Close-range vertical photography for measuring cover changes in perennial grasslands

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Abstract

We describe a method of close-range vertical photography and digital image analysis for measuring changes in total projective cover in perennial tussock grasslands of semi-arid Australia. Repeated photographs of permanent plots (1 m²) were classified using supervised image analysis, providing a clear and objective record of the effects of single-burns on grass cover relative to controls. Computer simulations of the photographic set-up indicated that errors due to camera perspective were consistently less than 4% across a range of cover classes. Other errors, including misclassification error, were not quantified because simplified laboratory tasks indicated that conventional field methods, such as point sampling and visual estimation, provided unreliable estimates of grass cover and were therefore not suitable benchmarks for assessing the photographic method. However, the presented data indicate that the photographic method was sufficiently accurate and precise to measure treatment effects over time and to elucidate relationships between independent growth parameters across a range of cover conditions. In addition, the photographic method was inexpensive, involved minimal field time, and utilised commercial software to classify images. It has the clear advantage over more traditional methods of providing outputs that are readily archived for retrospective studies.

Key Words: bunch grass, northwest Australia, permanent quadrats, prescribed burning, rangelands, *Themeda triandra* Forsskal

Traditionally, the methods employed in rangeland programs for monitoring changes in herbaceous cover have included visual assessment, point sampling, or transects. However, the fine-texture of grasses and the frequently large areas to be assessed lead to errors in estimation that are either large, unknown or observer-specific (Walker 1970, Sykes et al. 1983). These problems are confounded in arid environments where the patchy nature of the vegetation produces infrequent recordings and, as a result, wide confidence intervals (Friedel and Shaw 1987). Large or unknown errors have the potential to mask early signs of change and are

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Resumen

Describimos un método de fotografía vertical de rango estrecho y de análisis de imagen digital para medir los cambios en la cobertura total proyectiva de pastizales perennes amacollados de la región semiárida de Australia. Fotografías repetidas de parcelas permanentes (1 m²) se clasificaron utilizando el análisis de imagen supervisada, proveyendo un registro claro y objetivo de los efectos de la quema simple en la cobertura de los zacates en relación a las parcelas control. Simulaciones computarizadas de las fotografías indicaron que los errores debidos a la perspectiva de la cámara fueron consistentemente menores al 4% a través del rango de clases de cobertura. Otros errores, incluyendo el error de clasificación equivocada, no se cuantificaron porque las técnicas simplificadas de laboratorio indicaron que los métodos convencionales de campo, tales como el muestreo de puntos y la estimación visual, proporcionaron estimaciones poco confiables de la cobertura de los zacates, y por lo tanto, no fueron una referencia confiable para evaluar el método fotográfico. Sin embargo, los datos que se presentan indican que el método fotográfico fue suficientemente certero y preciso para medir los efectos de los tratamientos a través del tiempo y elucidar relaciones entre los parámetros independientes de crecimiento a lo largo de un rango de condiciones de cobertura. Además, el método fotográfico fue barato, requirió un tiempo mínimo en el campo y utilizó programas computacionales comerciales para clasificar las imágenes. Este método tiene la clara ventaja sobre los métodos tradicionales de proveer salidas fácilmente archivables para utilizarlas en estudios retrospectivos.

even more problematic where field data is scaled up, for example, in calibrations of remotely sensed data. Equally, variable errors are undesirable in experimental situations where accuracy and precision are required to differentiate natural variation from treatment effects (Kennedy and Addison 1987, Buttler 1992, Stampfli 1992).

Previous authors have discussed the potential of close-range vertical photography (Cooper 1924, Owens et al. 1985) and digital imaging (Roshier et al. 1997) to measure changes in vegetation cover over small areas. However, these techniques were either equipment-intensive (Roshier et al. 1997) and time-consuming (Owens et al. 1985) or were too early to take advantage of automated and objective image analysis (Cooper 1924). None were supported by systematically collected data.

Our objective was to demonstrate the use of close-range vertical photography and computerised image analysis in measuring changes in total cover of perennial tussock grasslands in semi-arid Australia. Using images of treatment plots over 2 years, we examined the potential of this method for providing objective measures of grass cover over a range of growth conditions. Relationships were described between cover across successive dates in permanent treatment plots and between cover and total biomass in temporary plots. Errors due to camera perspective were estimated using computer models of the photographic set-up. Finally, to evaluate the potential of more traditional methods for providing estimates of 'true' grass cover against which the photographic method could be assessed, we quantified errors in point sampling and visual estimation using highly simplified laboratory tasks.

Materials and Methods

Study sites

Two study sites, 11 km apart, were located on Hamersley Station (22°17'S 117°40'E) in the remote Pilbara region, northwest Australia (about 1,700 km north of the laboratory in Perth). The station occupies 224,000 ha, has been a pastoral lease since 1878, and currently runs 5,000 to 6,000 cattle. The climate is sub-tropical and semi-arid. Annual rainfall is 356 ± 153 mm (81-year mean \pm SD) falling on an average of 28 days mainly after summer cyclones (December to February). Air temperatures range from warm in winter (mean minimum and maximum of 11 and 24°C in July) to hot in summer (mean minimum and maximum of 26 and 40°C in January). Mean soil temperatures at 5 cm depth typically exceed 30°C from October to March with mean maxima greater than 40°C for the same months as measured from 1996 to 1998 at 1 site. Both sites were flat with soils derived from Quaternary alluvium. Soils were vertisols characterised by red swelling clays underlain by calcrete at about 60 cm depth.

Sites were located within perennial tussock grasslands dominated by a single species, kangaroo grass (*Themeda triandra* Forsskal), with ephemeral forbs less than 3% by weight (L.T. Bennett and M. A. Adams, unpublished data). Basal cover, of about 15%, was uniformly distributed across each site with litter concentrated around tussocks and with predominantly bare soil between tussocks. Both sites were more than 2.5 km from the nearest

water source and were of good range condition with no obvious erosion features associated with degradation (Tongway and Hindley 1995). Perennial tussock grasses, or 'bunch' grasses, are widely distributed throughout tropical, sub-tropical, and temperate Australia in a range of vegetation types. Kangaroo grass is a warm season perennial, characterised by tall flowering stems (up to 2 m), that occurs in all Australian states and in parts of South Africa and eastern Asia (Moore 1970). Kangaroo grass is often managed by regular burning in temperate and tropical zones but the use of prescribed fire in semi-arid regions such as the Pilbara has not been fully evaluated.

Treatment and plot design

A single experimental area of 1 ha was fenced at each site to exclude grazing. Treatment plots of 5 x 5 m were randomised in 4 complete blocks and were separated by 5 m buffer zones. 'Burn' and control plots were randomly distributed amongst 5 other treatments involving single and combined additions of N and P (50 kg ha⁻¹ N, 25 kg ha⁻¹ P) and additions of water either alone or with a combined NP addition. To examine interactions between block and treatment (Underwood 1997), we included an additional random replicate of both control and 'burn' treatments in each block, increasing the total number of treatment plots at each site to 36 ((2 treatments x 4 blocks x 2 replicates) + (5 treatments x 4 blocks)). Since our primary aim was to demonstrate and evaluate the photographic method rather than to interpret treatment effects, we have included all data from control and 'burn' plots because it was the most complete data set. Examination of effects of nutrient and water additions was beyond the scope of this paper and only limited data from these treatments were included to illustrate relationships between biomass and cover (see below).

'Burn' plots in the same block were ignited in sequence over 2 consecutive evenings in late November 1996 (1 evening per site). During burning, wind speeds were negligible, air temperatures ranged from 31 to 38°C and relative humidity was 9 to 15%. Plots were ignited on all sides and fire consumed all above-ground biomass within 2 to 4 min, leaving a minimal cover of ash around tussock bases. Flame heights, monitored using video recording, were consistently less than 1 m and there was no increase in soil temperatures at 2 cm depth for the duration of the burns.

The first rain of a wet summer (494

mm) fell about 20 days after burning and, by March 1997, most of the burnt tussocks had successfully recovered. An extended dry period followed (130 mm from March 1997 to February 1998 inclusive), before an average autumn (115 mm from March to May 1998) and an above-average winter (202 mm from mid-June to August) in 1998 (data from 2 stations within 2 to 32 km of sites).

Photography and image analysis

A single permanent sub-plot of 1 x 1 m was established at the center of each treatment plot. These sub-plots were marked by 2 steel 'locating rods' in diagonally opposite corners which allowed a portable 1 m² quadrat, mounted on legs, to be accurately placed at each sampling date (Fig. 1).

The permanent sub-plots were photographed using close-range vertical photography on 5 October 1996 (before treatment), 2 December 1996 (burnt only), 21 March 1997 (after good summer rains), 29 June 1997, 12 November 1997, 6 June 1998 (after an extended dry period), and 1 October 1998 (after good winter rains). At each date (except June 1998), an equivalent 'biomass' sub-plot (1 m²) was photographed in the surrounding treated area prior to complete harvest. All permanent sub-plots were photographed at each date but the number of 'biomass' sub-plots ranged from 2 to 4 per treatment per site according to logistical constraints of each sampling trip. Biomass was not sampled in June 1998 because heavy rains prevented further access to sites. Samples were separated in the field into litter, ephemeral forbs and standing kangaroo grass. After drying (75°C for 48 hours) and weighing, a sub-sample of the standing kangaroo grass (about 30% by mass) was further sorted into green foliage, standing dead foliage, persistent 'crowns' at tussock bases, flowering stems and seed heads. Limited data from 'biomass' sub-plots were included here to examine relationships between total projective cover and total aboveground biomass, and to aid interpretation of cover changes in permanent sub-plots using, for example, proportional changes in biomass components. Detailed analysis of treatment effects on biomass components will not be presented here.

Photographs were taken with a 35 mm SLR camera (Canon EOS 100, Canon Inc., Tokyo, Japan) fitted with a 35 mm lens. The camera was mounted, at 2 m height, on a portable, self-supporting aluminium stand (Fig. 1) equipped with a collapsible camera arm and 2 telescopic legs for ease of transport. Bubble levels were used to

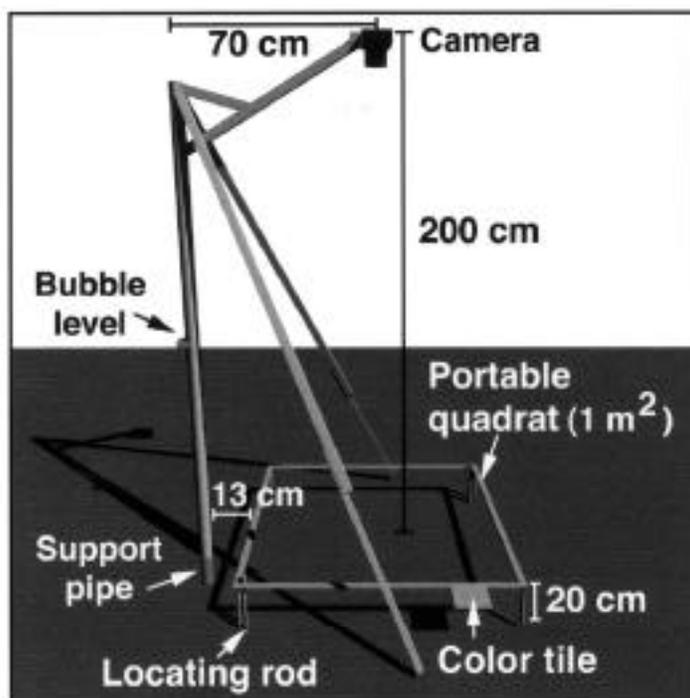


Fig. 1. Schematic diagram of the photographic set-up. The camera was mounted using a quick-release mechanism and its vertical position was checked by placing a hand-held bubble level against the camera lens (not shown). The support pipe and 2 locating rods (in diagonally opposite corners) were permanently placed to mark the location of permanent sub-plots. The camera stand was attached to a base-plate when photographing temporary 'biomass' sub-plots.

ensure that the stand, camera, and resulting images were vertical. Using standard slide film (negative dimensions 24 x 36 mm) and a camera focal length of 35 mm, the imaged area, of about 1.4 x 2.1 m, adequately covered a 1 m² sub-plot. A lesser focal length (for example, 28 mm) would increase the angle of coverage but would increase lens distortion, whereas a greater focal length (for example, 50 mm) would decrease distortion but would require a less practical camera height of about 3 m to cover the same ground area. To ensure uniform lighting, the sub-plot and surrounding area was shaded with a screen of close-mesh cloth and a flash was used. A tile with a number of colored squares ('color tile', Fig. 1) was attached to the side of the portable quadrat to assist with color correction of images during later editing. Images were captured on 100 ASA color slide film (Sensia II 100, Fuji Photo Film Co., Ltd., Tokyo, Japan). One person could easily manage the camera stand and 2 persons could comfortably photograph a whole site of 36 permanent sub-plots within 2 to 2.5 hours.

The central 24 x 30 mm of each slide, which included the outer-edges of the quadrat and the color tile, was scanned using a high resolution film scanner

('Nikon LS-1000', Nikon Inc., Melville, N.Y., optical resolution 2,400 dpi), to create a 600 x 750 pixel image at 72 dpi. These raw images were saved as uncompressed JPEG files and were edited and analysed using Adobe Photoshop (Adobe Systems Inc., San Jose, Calif.). Individual images were subsequently adjusted for color by using the black, white, and grey points on the color tile, and by increasing both contrast and brightness by 50%. The area defined by the internal edges of the quadrat (1 m²) was copied and rescaled to give a final image size of 500 x 500 pixels. Thus, each pixel represented a ground area of about 2 x 2 mm.

Images were analysed for cover in batches according to site and date to accommodate changes in soil brightness and lighting conditions. Total projective plant cover, including standing kangaroo grass and the minor components of litter and ephemeral forbs, was estimated by selecting and deleting soil-colored pixels as follows:

1. Two control and 2 'burn' images, representing the full range of cover for that site and date, were combined in one image (that is, 1,000 x 1,000 pixels).

2. The combined image was converted from 24-bit (2²⁴ or millions of colors) to 8-bit (2⁸ or 256 colors) to create a custom 'Color Look Up Table' (CLUT) that was weighted towards the spectrum of the image.
3. All images were converted to 8-bit color using the custom CLUT created in step 2.
4. Soil colors (in this case browns and reds) were selected from the CLUT to create a customised color range.
5. Pixels within this color range were selected and recolored white, the remaining pixels (that is, plant cover) were recolored black (Fig. 2) and the percentage of black pixels was recorded.

Using Photoshop's automated 'action' and 'batch' commands (version 4 or later), 36 cropped images could be analysed for total cover in less than 90 min. This time included visual checks for accuracy by comparing classified images with raw images.

Errors in photographic method

Since cover was estimated using images taken from a single camera point, we expected some errors due to displacement associated with tussock height and to lens distortion. We estimated these errors across a range of covers using computer-generated 3-D models. We compared vertically-projected 'model' cover with cover estimated from the perspective of a virtual 'camera'. Virtual 'tussocks' were constructed using a 3-D animation package (Specular Infini-D, Specular International Ltd., Amherst, Mass.) and were designed according to field-observations of leaf length (maximum 30 cm) and leaf angle (most < 45° from the horizontal). Each virtual 'tussock' consisted of 28 identical flat, linear 'leaves' joined at the base and arranged evenly around the central axis at a range of angles (6 'leaves' at each of 15, 30, 45, and 60° and 4 leaves at 75° from the horizontal). We created a range of 'tussock' sizes by varying the length of constituent 'leaves' between 10 and 30 cm. Varying numbers of 'tussocks' were randomly arranged within a scaled 2 x 2 m area, within which a 1 x 1 m 'quadrat' was centrally located at a height of 20 cm. A virtual 'camera', configured to simulate a 35 mm SLR camera with a 35 mm lens, was positioned at 2 m height directly above the central 1 m² 'quadrat'. That is, the set-up of the virtual 'camera' was a geometrically accurate model of the field set-up (Fig. 1) and the distortion and displacement modeled by the virtual 'camera' was equivalent to that associated with the real camera in the field.

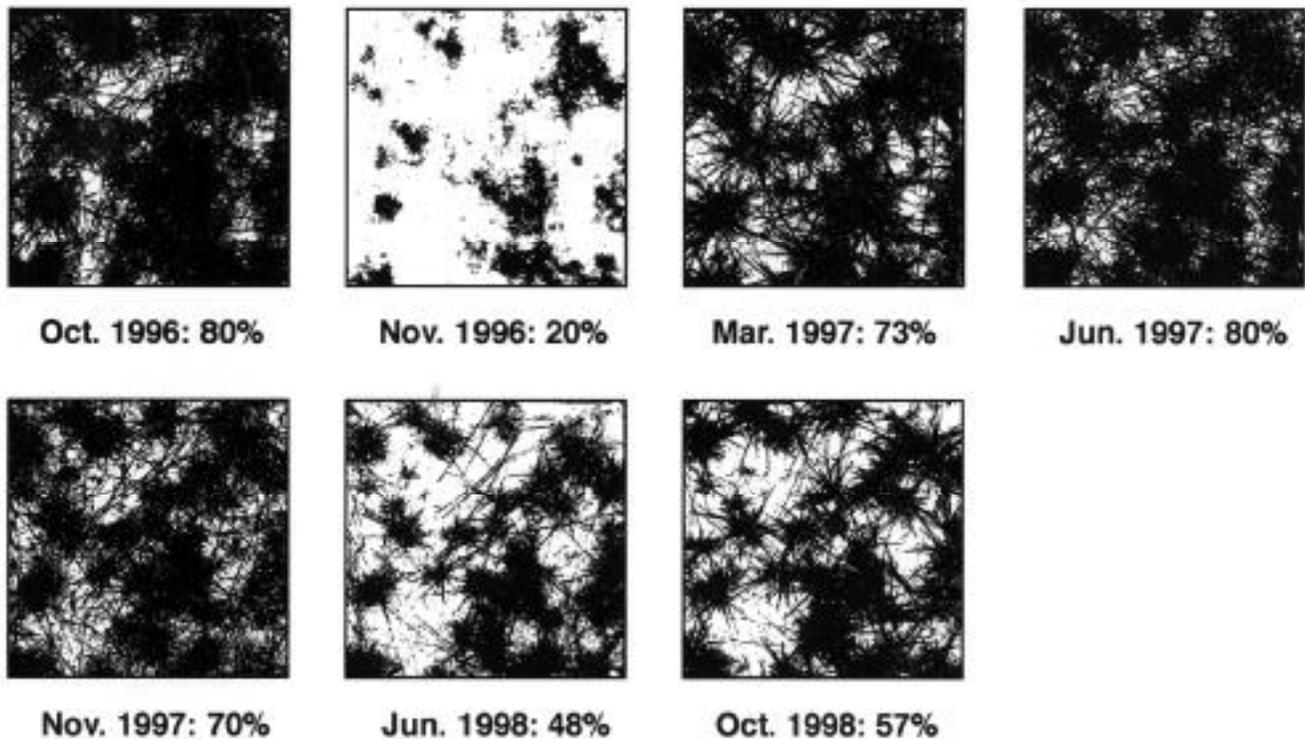


Fig. 2. Sequence of classified images of the same permanent 'burn' sub-plot showing seasonal changes in total projective cover (that is, standing kangaroo grass and the minor components of litter and ephemeral forbs). Burns were conducted in November 1996.

Two 'images' of the modeled 2 x 2 m area were generated—the first was a direct vertical projection at 20 cm height (used for 'model' cover), and the second a 'camera' view (for 'estimated model' cover). Each 'image' was cropped to the internal edges of the central 'quadrat' before measurement of total cover using color discrimination of 'tussock' and background pixels. To reflect frequency distributions of cover in the field, this procedure was repeated 5 times in each of 5 cover classes (20 to 40%, 40 to 60%, 60 to 70%, 70 to 80%, and 80 to 90%) giving a range of 'model' covers from 25 to 88%. The lower limit was near that measured in the field and the upper limit was restricted by the number of tussocks that could physically fit within the 2 x 2 m area. Thus, while not an exact representation of field conditions because, for example, the distribution of litter around tussock bases was not simulated, the model allowed examination of potential error across a range of cover conditions. We did not examine errors due to topographic displacement, since both sites in this study were flat; however, we envisage that the camera attachment could be adapted to allow rotation so that the camera was positioned parallel with the main slope while the stand was kept on a vertical plane.

Additional errors in the photographic method included the misclassification of pixels. We considered these errors to be minimal as soil and plant colors were easily distinguished and classified images were carefully checked for accuracy against raw images. Quantifying total error, including misclassification error, would require a measure of 'true' cover against which the photographic method could be assessed. Preliminary evaluations at the study sites indicated that traditional field estimates of cover, such as point sampling and visual estimation, were prone to errors associated with observer subjectivity and inconsistency and could not provide reliable cover estimates. Further analysis of point sampling and visual estimation, using greatly simplified tasks in the laboratory (see below), confirmed that these methods were unreliable and could not be used to 'truth' our estimates of grass cover. Instead, we used indirect indicators to illustrate the photographic method's accuracy and precision, such as the strength of relationships between biomass and photographic cover in 'biomass' sub-plots, and between photographic cover on successive sampling dates in permanent sub-plots (given that the cover estimates from each date were independently derived using date-specific color tables).

Errors in other methods of cover estimation

As mentioned above, we assessed the potential errors in 2 traditional field measures of cover—point sampling and visual estimation—using simplified tasks in the laboratory. This involved estimating the 'cover' of black pixels in classified black-and-white images of permanent 1 m² sub-plots (Fig. 2). Classified images were used because they contained the same fine-textured patterning as quadrats in the field, and because, unlike raw images, the actual 'cover' was known, allowing an exact calculation of the accuracy of each estimate ('percentage black' minus 'estimated percentage black'). As such, the measured errors were conservative because the use of 2-dimensional, duo-tone images would decrease errors due to, for example, observer fatigue and observer perspective in the field.

Five classified images ('replicates') from each of 6 cover classes (20 to 40%, 40 to 60%, 60 to 70%, 70 to 80%, 80 to 90%, and 90 to 100%) were chosen to reflect frequency distributions of cover in the field, giving a range of 'percentage black' from 22 to 97%. To assess point-sampling, sets of random 'points' were generated using a purpose-built computer program. Each 'point' was a single pixel (out of a total 250,000 pixels per image)

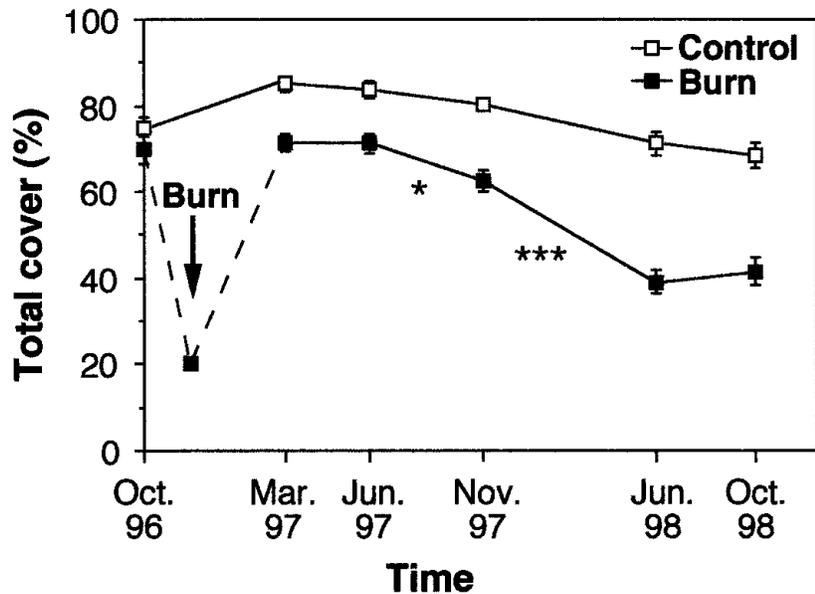


Fig. 3. Changes in total projective cover (including standing kangaroo grass and minor components of litter and forbs) in permanent sub-plots of control and 'burn' treatments. Values are means across site and block (n = 16; bars = SEM). Asterisks indicate significant differences between treatments in the change in cover between 2 successive dates (**** significant at $P \leq 0.05$ and 0.001, respectively).

equivalent to a ground area of 2 x 2 mm. For each of the 30 test images, 5 sets of each of 10, 20, 50, 100, 200, 500, and 1,000 points were sampled (a total of 35 sets per image). The points in each set were classified as either black or white and the 'estimated percentage black' calculated. For visual estimation of cover, the same 30 test images were printed for observation by 5 trained ecologists with similar practical experience of herbaceous cover estimation. Images were sampled at random for inclusion in 2 'arrangements' each comprised of 6 images on 5 pages. Before estimating the 'cover' of black pixels for each arrangement, each observer studied 6 black-and-white images illustrating the full range of covers. These reference images were then removed and covers of test images were estimated, to the nearest 1%, at the observer's leisure (typically 20 seconds per image).

Statistical analyses

Effects of treatment (control vs 'burn'), site, and block on changes in photographic cover of permanent sub-plots between 2 successive sampling dates were tested using the difference in cover as the dependent variable in an analysis of variance with block nested within site. Since permanent sub-plots were repeatedly photographed, the additional effect of sampling date was tested using cover as the

dependent variable in a multivariate repeated measures analysis of variance (after Rowell and Walters 1976, Green 1993). Relationships between cover and biomass in 'biomass' sub-plots, and between cover in permanent sub-plots

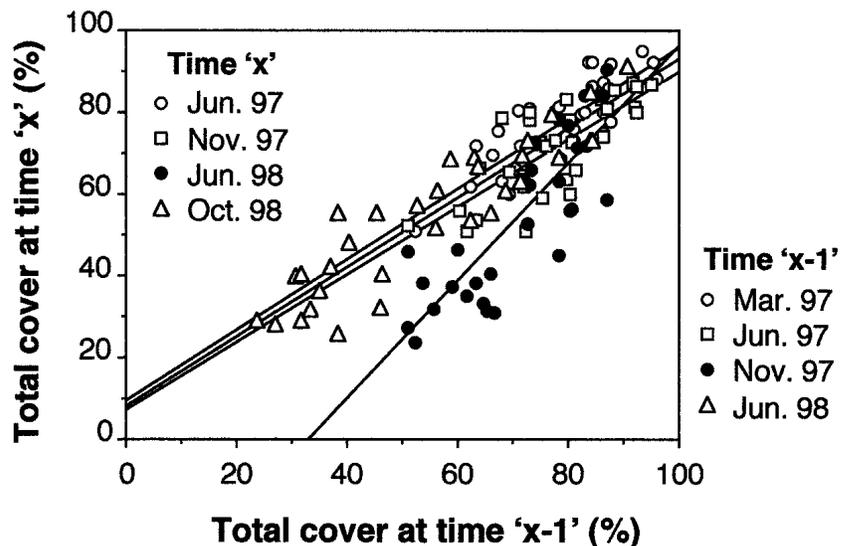


Fig. 4. Relationships between total projective cover in permanent sub-plots at any sampling date (time 'x') and total cover at the previous sampling date (time 'x-1'). The slope and intercept of the regression line between covers in June 1998 and November 1997 (black circles) were significantly different ($P < 0.001$) from other regressions ($Y = -47.2 + 1.4 X$; adjusted $r^2 = 0.71$). Regression lines where time 'x' represented June 1997, November 1997 and October 1998 were not significantly different (combined regression: $Y = 8.0 + 0.9 X$; adjusted $r^2 = 0.81$). The relationship between cover in March 1997 and October 1996 was removed for clarity because data were clustered in the top right corner.

across successive dates, were examined using scatter plots. Differences between regression lines were tested using co-variate analysis.

Effects of cover class on simulated photographic error were tested using the difference between 'model' and 'estimated model' cover in a single factor analysis of variance. For point sampling of classified images, effects of cover class, replicate, and number of points on absolute differences between 'percentage black' and 'estimated percentage black', were analysed using a partially nested analysis of variance with replicate nested within cover class. A similar model was used to examine effects of cover class, replicate, observer, and image arrangement on visual estimates of 'percentage black' in classified images. All analyses used the models of SuperANOVA (Abacus Concepts, Inc., Berkeley, Calif.).

Results and Discussion

Treatment and seasonal effects measured using photographic method

Images of the permanent sub-plots provided a clear record of seasonal changes in growth form and cover of the perennial grasses. Most images showed excellent discrimination between soil and plant material and cover estimates were easily

obtained using the described image-analysis technique. A sequence of classified images from a 'burn' plot (Fig. 2) clearly illustrated both the recovery of tussocks after fire and the periods of growth and decline. Tussocks were compact with relatively upright foliage (maximum length 30 cm) during periods of active growth (March 1997 and October 1998). As the time since rain increased (June 1997 to June 1998), tussocks were reduced to low, rounded hummocks (leaf length 15 cm). Litter was consistently concentrated around tussock bases, leaving open spaces between tussocks at all dates, and averaged 10% of aboveground biomass for the study period (data from control 'biomass' sub-plots). Ephemeral forbs were never more than 3% of aboveground biomass and typically contributed less than 1% of total plant projective cover. Tall flowering stems, produced after the summer rains of 1996/97, were flattened by strong winds and added to projective cover while they persisted (June 1997 and November 1997). Movement of these stems sometimes affected image clarity; the problem was only significant in 'N-added' sub-plots where stem biomass and height were significantly increased after summer rains (L. T. Bennett and M. A. Adams, unpublished data).

The utility of an objective and consistent method for estimating total projective cover was demonstrated by clear treatment effects through time (Fig. 3) and strong relationships between cover on successive dates (Fig. 4). Using multivariate repeated measures analysis of variance, we detected significant effects of both treatment ($P < 0.001$) and sampling date ($P < 0.001$) on total cover in permanent sub-plots (effects of site and block were insignificant in all analyses). Burning reduced total projective cover at all sampling dates (Fig. 3). Moreover, a significant interaction between treatment and date indicated that cover in 'burn' and control sub-plots responded differently to seasonal changes. For example, decreases in cover between June 1997 and November 1997 and between November 1997 and June 1998 were significantly greater in 'burn' sub-plots relative to control sub-plots using the difference in cover between 2 dates as the dependent variable in an univariate analysis of variance. It seems likely that removal of cover by burning increased the exposure of plants during the hot and abnormally dry summer of 1997/98 (December 1997 to February 1998). Retained cover in control sub-plots provided direct 'insulation' or otherwise ame-

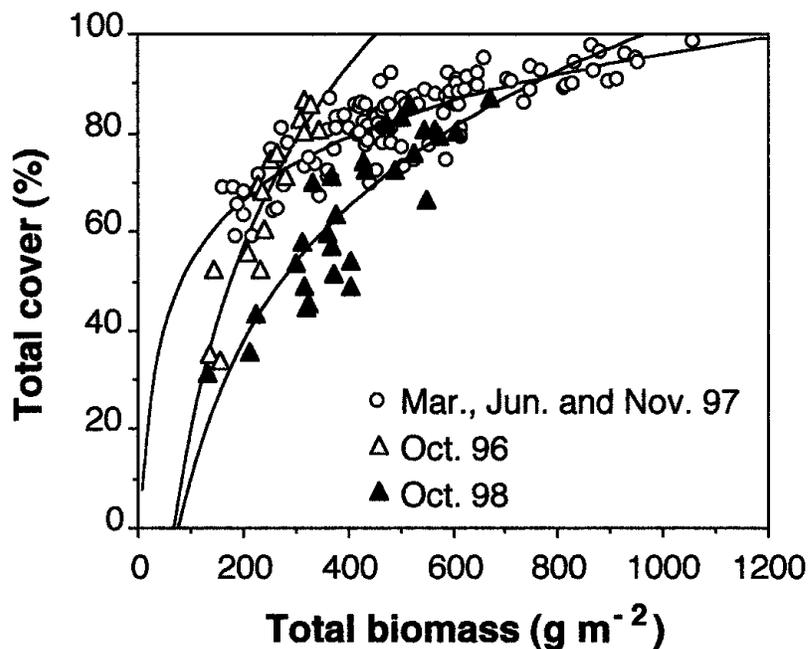


Fig. 5. Relationships between total projective cover and total aboveground biomass (that is, standing kangaroo grass, litter and ephemeral forbs) in 'biomass' sub-plots. In order to increase the range covered, data were from control and 'burn' treatments and from treatments involving additions of nutrients and water. Lines of best fit were logarithmic (shown) and were not significantly different for the 3 dates in 1997 ($Y = -30 + 42 \log X$; adjusted $r^2 = 0.72$). Relationships were different for October 1996 ($Y = -224 + 122 \log X$; adjusted $r^2 = 0.83$) and October 1998 ($Y = -172 + 91 \log X$; adjusted $r^2 = 0.74$).

liorated local microclimate, and helped to prolong leaf function and residence time in an extremely arid environment. This interpretation was supported by relationships between cover near the start of summer in November 1997 and at the next sampling date in June 1998 (Fig. 4). The slope of the regression for these 2 dates was significantly greater than for other consecutive dates. A simple and clear explanation is that where cover before the onset of the hot dry summer was less than 70% (as it was in most 'burn' sub-plots), subsequent changes in cover were greater than in periods of less severe weather. Since data from 'burn' sub-plots were included to demonstrate the potential of the photographic method in monitoring treatment effects through time (Austin 1981), a detailed interpretation of treatment effects is not included here and is the subject of ongoing research.

Strong relationships between projective cover and total aboveground biomass (Fig. 5) indicated the accuracy of cover estimates from image analysis and demonstrated the method's practical application. The strength of these relationships was probably due to the predominance of a single grass species and the relative absence of spreading forbs. However, as in other studies of perennial grasslands (Friedel

and Shaw 1987), there was no universal relationship between cover and biomass. Instead, relationships varied according to the time of sampling, with different equations for October 1996, March to November 1997, and October 1998 (Fig. 5). These equations represented growth in different seasons within different years, following rains in autumn 1996, summer 1996/97 and winter 1998, indicating that relationships between cover and biomass were 'fixed' between periods of growth and that the form of the relationship was determined by the season of rain and the magnitude of growth responses. For example, less cover was required to produce up to 400 g m⁻² of biomass in October 1998, after good winter rains, than in other months (Fig. 5). The different form of the relationship in October 1998 was probably due to a combination of the greater proportional mass of green foliage relative to all other dates (17% vs 12%, data from 'biomass' sub-plots) and the more upright orientation of foliage (see Fig. 2). These characteristics were, in turn, due to the season of growth—to the favourable conditions for new growth associated with 'effective' winter rainfall and to the above-mentioned effects of the preceding dry period on other components of the standing biomass. These data indicate that

Table 1. Absolute difference (%) between actual and estimated cover for each of 3 cover methods. Actual cover was 'model' cover for the virtual 'camera', and 'percentage black' for point sampling and visual estimation. Values are across all observations of individual actual covers and by actual cover classes.

Method	All observations				Cover class (%)					
	n	x	SD	Range	20–40	40–60	60–70	70–80	80–90	90–100
Virtual 'camera' ¹	25	(%) 4	1.3	(%) 1–7	3	4	4	(%) 5	4	–
Point sampling ²										
10 points	150	10	7.4	0–33	11	12	11	12	10	6
20 points	150	8	6.5	0–31	7	10	9	7	7	5
50 points*	150	4	3.3	0–20	4	4	6	5	3	3
100 points**	150	3	2.6	0–16	3	4	4	2	3	2
200 points***	150	2	1.8	0–9	2	3	3	2	2	1
500 points**	150	2	1.1	0–6	2	2	2	1	1	1
1,000 points**	150	1	0.9	0–5	2	2	1	1	1	1
Visual estimation ²										
All observers (n = 5)***	300	7	6.4	0–30	6	10	9	6	4	4
Most accurate observer	60	4	3.6	0–13	4	5	7	3	3	2
Least accurate observer**	60	14	8.3	0–30	11	20	18	16	10	7

¹All 'estimated model' covers were less than 'model' covers (by 4% on average). 'Model' cover ranged from 25 to 88% and was the vertically projected cover of computer models of grass tussocks in a 1 m² quadrat. 'Estimated model' cover was measured using a virtual 'camera' (35 mm lens) at 2 m above the center of each simulated quadrat.

²'Percentage black' ranged from 22 to 97% and was the percentage of black pixels in classified images of 1 m² treatment sub-plots. 'Estimated percentage black' was measured by computerised point sampling or by visual estimation using the same classified black-and-white images.

*, **, *** Significant effect of cover class at P = 0.05, 0.01, and 0.001, respectively.

substantial errors may result from assuming consistent relationships between total cover and total biomass. Estimates of productivity from cover at large scales should therefore take into account measures of grass form (for example, foliage orientation) and of the proportional mass of green material (analogous to measures of greenness in satellite imagery, Pickup et al. 1994).

Errors in estimates of cover and advantages of photographic method

Using computer models of grass 'tussocks' and a virtual 'camera', we found a linear relationship, with a slope near unity, between 'estimated model' cover (using a 'camera' view) and 'model' cover (direct vertical projection at 20 cm height). The relationship between these measures was strong ('estimated model' = -2.09 + (0.97 'model'); adjusted r² = 1.00), as might be expected, and clearly demonstrated that 'estimated model' cover was always less than 'model' cover, with differences averaging 4% (range from 1 to 7%) irrespective of cover class (Table 1). These data show that perspective errors associated with the photographic method were constant and that they could be accounted for through systematic adjustment. Alternatively, cover estimates from the photographic method would not need to be adjusted for perspective in many experimental situations where relative rather than absolute differences between, for example, treatments or sampling dates, were of interest.

In contrast to the consistency of perspective errors in the photographic

method, errors using point sampling or visual estimation of classified images were significantly different between cover classes (Table 1). On average, absolute differences between 'percentage black' and 'estimated percentage black', using either of these methods, were greatest where 'percentage black' was 40 to 60% or 60 to 70% and least where 'percentage black' was 90 to 100% (Table 1). This is consistent with field studies by Sykes et al. (1983) that errors in visual estimates of ground cover were greatest near covers of 50% and least at the extremes of 0 and 100%. While such heterogeneity of error can be reduced by angular transformation of cover data, significant interactions between observer and cover class (P < 0.01, see also Sykes et al. 1983), imply considerable difficulty in adjusting for errors across a range of covers if estimates are made by more than 1 observer.

The observer had a significant effect on visual estimates of cover in classified images, with average differences between 'percentage black' and 'estimated percentage black' ranging from 4 to 14% and estimates of 'percentage black' in individual test images out by as much as 30% (Table 1). Averaged across all observers, errors here were low (7%) when compared with the 10 to 20% accuracy expected in field studies (Sykes et al. 1983, Kennedy and Addison 1987), reflecting the simplified task of estimating cover in 2-dimensional, duo-tone images. The arrangement of images did not significantly affect accuracy of visual estimates, but there were significant interactive effects between

observer and image arrangement (P < 0.05) and between cover class and image arrangement (P < 0.05); further evidence that errors associated with this method are unpredictable. For point sampling, the effect of point number on accuracy was highly significant (P < 0.001). Differences between 'percentage black' and 'estimated percentage black', across all observations, were significantly greater using 10 compared to 20 points (10 vs 8%), 20 compared to 50 points (8 vs 4%), 50 compared to 100 points (4 vs 3%), and 100 compared to 1000 points (3 vs 1%, Table 1). Using this highly simplified evaluation of point sampling, 100 or more points per 1 m² quadrat would be required to estimate total projective cover to within less than 5% across a range of cover classes. We would expect the required number to increase to at least 200 points in the field given additional sources of error due to inconsistencies associated with observer fatigue and observer perspective (that is, observation of points from oblique angles rather than directly above). This level of sampling could equate to as much as 4 field hours per quadrat (Stampfli 1991) and might be compared to the capacity to take 36 photographs within 2.5 hours using the photographic method described here.

The variable error of both the visual estimation and point sampling methods in simplified laboratory tasks, supported our preliminary conclusion that neither technique could provide measures of 'true' grass cover against which the photographic method could be assessed. Orthophotos,

produced from stereoscopic pairs of sub-plot images, could provide a more accurate benchmark and will be compared with single images in future research. However, data presented here would indicate that the photographic method is sufficiently accurate and precise to measure treatment effects over time (Fig. 3), and to elucidate relationships between growth parameters across a range of conditions (Figs 4 and 5). Furthermore, the described photographic method captured and analysed images with ease and speed. Thus, a large number of small plots could potentially be measured either as contiguous plots in intensive studies or as single plots in nested designs over large areas (Stohlgren 1995, Stohlgren et al. 1998). Since the images were easily archived, data could be used in retrospective studies that examined new questions or that utilised improvements in interpretative tools such as image analysis procedures (Pace and Cole 1989). Finally, the use of objective color analysis to discriminate between plant and soil clearly suits the red soils and discontinuous litter of these sites and other sites within arid and semi-arid zones. Further evaluation of the method would be required to assess its potential in other herbaceous communities that are more diverse and structurally complex or that occur on different colored soils. Where distinguishing plant from soil is a problem, we suggest the trial of discrimination parameters using primary color values or intensity measures (Pan et al. 1998) or the use of wavelengths beyond the visible range such as infra-red.

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Lichen polysaccharides and their relation to reindeer/caribou nutrition

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Abstract

Samples of *Cetraria islandica*, *Cetraria nivalis*, *Cladina stellaris*, *Cladina arbuscula*, *Cladina rangiferina* and *Stereocaulon paschale* were collected at 3 sites in 2 mountain areas in Norway. *Alectoria ochroleuca* was collected at 3 sites in 1 of the mountain areas. Lichens contained between 83 and 93% fiber, measured by the dietary fiber analysis, with *Cladina* spp. containing significantly more fiber than the other lichen species. The fiber consisted mainly of mannose, galactose, and glucose, but the relative content of each monosaccharide differed between species. Fibers from *Cetraria* spp. and *Alectoria ochroleuca* contained significantly more glucose than those from *Cladina* spp. and *Stereocaulon paschale*, while *Cladina* spp. and *Stereocaulon paschale* contained significantly more mannose and galactose. The higher glucose content in *Cetraria* spp. and *Alectoria ochroleuca* was reflected in a high lichenan content in these species, while the *Cladina* spp. and *Stereocaulon paschale* contained no lichenan. Solubility of the fiber fraction in hot water was strongly correlated to lichenan content, and great differences existed between species. Less than 5% of the dietary fiber was soluble in lichens of the *Cladina* genus, while more than 50% of the fiber was soluble in *Cetraria islandica* and *Alectoria ochroleuca*. Twenty-one percent of the dietary fiber was soluble in *Cetraria nivalis*. In vitro gas production experiments using rumen inocula from reindeer revealed a higher gas production rate the first 5 hours of incubation in *Cetraria islandica*, *Cetraria nivalis*, and in *Alectoria ochroleuca* compared to *Cladina* spp. and *Stereocaulon paschale*. Maximum production rate was observed at about 13 hours and dropped rapidly thereafter. No systematic differences in gas production rate between lichens species were observed after the initial phase. Differences in gas production rate in the initial phase resulted in higher total gas production in *Cetraria islandica*, *Cetraria nivalis* and in *Alectoria ochroleuca* compared to *Cladina* spp. and *Stereocaulon paschale* the first 9 hours of incubation. Total gas production after 52 hours of incubation did not vary between species. Gas production characteristics indicate that the amount of readily fermentable fraction was greater, whereas the amount slowly fermentable fraction was lower in lichens of the *Cetraria* genus and in *Alectoria ochroleuca* compared to *Cladina* spp. and *Stereocaulon paschale*. The water-soluble fraction is easy available for rumen micro-organisms and the results indicate a close relationship between high gas production in the initial phase and high proportion of water soluble fibers and/or lichenan content. Content, composition, and solubility of the fiber fraction could thus be potentially important factors determining nutritive value of the lichen for reindeer/caribou.

Key Words: *Cetraria* spp., *Cladina* spp., *Alectoria ochroleuca*, *Stereocaulon paschale*, dietary fiber, lichenan, in vitro gas production

Resumen

Se colectaron muestras de *Cetraria islandica*, *Cetraria nivalis*, *Cladina stellaris*, *Cladina arbuscula*, *Cladina rangiferina* y *Stereocaulon paschale* en 3 sitios de 2 áreas de montañosas de Noruega. Se colectó *Alectoria ochroleuca* en 3 sitios de una de las áreas montañosas. Los líquenes contenían de 83 a 93% de fibra, medida por el análisis de fibra dietaria, las especies de *Cladina* tenían significativamente más de fibra que las otras especies de líquenes. La fibra consistió principalmente de manosa, galactosa y glucosa, pero el contenido relativo de cada monosacárido difirió entre especies. La fibra de las especies de *Cetraria* y *Alectoria ochroleuca* contenían significativamente más glucosa que la fibra de las especies de *Cladina* y *Stereocaulon paschale*, mientras que la fibra de las especies de *Cladina* y *Stereocaulon paschale* tenía más manosa y galactosa. El alto contenido de glucosa de las especies de *Cetraria* y *Alectoria ochroleuca* se reflejó en un mayor contenido de liquenan en estas especies, mientras que las especies de *Cladina* y *Stereocaulon paschale* no contenían liquenan. La solubilidad en agua caliente de las fracciones de la fibra estuvo fuertemente correlacionada al contenido de liquenan y existen grandes diferencias entre especies. En las especies de *Cladina*, menos del 5% de la fibra dietaria fue soluble mientras que en las especies *Cetraria islandica* y *Alectoria ochroleuca* más del 50% de la fibra fue soluble y 21% de la fibra dietaria fue soluble en *Cetraria nivalis*. Experimentos de producción de gas *in vitro* utilizando inoculo ruminal de reno revelaron una alta tasa de producción de gas en las primeras 5 horas de incubación de *Cetraria islandica*, *Cetraria nivalis* y *Alectoria ochroleuca* comparado con las especies de *Cladina* y *Stereocaulon paschale*. La máxima tasa de producción de gas se observó a las 13 horas y a partir de aquí disminuyó rápidamente. Después de la fase inicial no se observaron diferencias sistemáticas entre especies de líquenes en la tasa de producción de gas. Las diferencias en la tasa de producción de gas en la fase inicial resultaron en una mayor producción de gas en las especies *Cetraria islandica*, *Cetraria nivalis* y *Alectoria ochroleuca* comparado con las especies de *Cladina* y *Stereocaulon paschale*, esto durante las primeras 9 horas de incubación. La producción total de gas después de 52 horas de incubación no varió entre especies. Las características de producción de gas indican que la cantidad de la fracción de rápida fermentación fue mayor en tanto que la cantidad de la fracción de lenta fermentación fue menor en los líquenes del género *Cetraria* y en *Alectoria ochroleuca* comparado con las especies de *Cladina* y *Stereocaulon paschale*. La fracción soluble en agua es de alta disponibilidad para los microorganismos del rumen y los resultados indican una estrecha relación entre la alta producción de gas en la fase inicial y una alta proporción de fibras solubles en agua y/o contenido de liquenan. El contenido, composición y solubilidad de las fracciones de la fibra pudieran ser factores potencialmente importantes en determinar el valor nutritivo de los líquenes para los renos y caribúes.

In winter, lichens are the principal fodder resource for reindeer/caribou throughout most of their range (Andreyev 1977, Eriksson et al. 1981, Russell and Martell 1984), especially mat-forming species of the genera *Cetraria* and *Cladina* when available (Andreyev 1977, Eriksson et al. 1981). In the taiga belt, the aboreal lichens *Usnea* spp. and *Bryoria* spp. may also play an important role in the winter diet (Andreyev 1977).

Due to high preference by reindeer, but slow potential growth rate (Andreyev 1977, Tveitnes 1980, Virtala 1992), lichens are vulnerable to overgrazing. Overgrazing reduces lichens density, but may also change the relative abundance of different lichen species, since their vulnerability to grazing and trampling varies (Klein 1987). Also their ability to recoup from over-utilisation varies (Andreyev 1977, Gaare & Skogland 1980, Klein 1987). Sound management of lichens is therefore essential in both wild reindeer and caribou management and in semi-domestic reindeer husbandry.

Lichens are considered to mainly consist of different carbohydrate fractions. However, little has been done to quantify the carbohydrate content in lichens of importance in reindeer nutrition. In addition, solubility of the fiber fraction may be a useful parameter, since it could influence the initial lag phase of rumen fermentation and hence influence lichen digestibility.

Early investigations have revealed that reindeer have a greater ability to digest lichens compared to, for example, sheep (Prestegge 1954). The higher capacity of reindeer and caribou to exploit lichens than other northern ungulates is a key factor in understanding their success throughout most of the circumpolar region. A more detailed knowledge of the composition of the most important lichen species is a prerequisite to determine factors involved in digestion of lichens in reindeer/caribou. This may have bearings for management of lichen ranges and in evaluation of quality and stocking capacity of these.

The objectives of this study were to quantify the carbohydrate composition and solubility of lichens, and to study the ruminal breakdown pattern of these lichens for reindeer.

Material and methods

Lichens of the species *Cetraria islandica* (L.), *Cetraria nivalis* (L.), *Cladina stellaris* (Opiz), *Cladina arbuscula* (Waller), *Cladina rangiferina* (L.) and *Stereocaulon*

paschale (L.) were collected from 3 randomly selected sites of alpine ridge vegetation in 2 mountain areas in central Norway; Jotunheimen (61° 10') and Hardangervidda (60° 30') in August 1996. In addition, *Alectoria ochroleuca* was collected from 3 sites in Hardangervidda. The samples were picked by hand by gently breaking off 1 to 3 cm of the upper dry part of the podetium. The reindeer grazing impact of the lichen mat was low to moderate at all sites.

The samples were air-dried and cleaned by hand for foreign substances. To meet the requirements for dietary fiber analysis, the samples were ground on a laboratory rotor mill fitted with a 0.5 mm screen. Dry matter (DM) was determined after drying at 105° C overnight, ash was determined after 4 hours at 550° C, and crude protein was determined as Kjeldahl N X 6.25. Crude fiber was analyzed according to the Weende method (Henneberg and Stohmann 1859), with the modification that 200 mg instead of 1 g was used to avoid viscosity problems during filtration. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) was analysed according to Van Soest and Wine (1967), with the amount of sample reduced to 150 mg. Starch content corrected for free glucose content was determined according to the method of McCleary et al. (1994). Total mixed-linked (1-3)(1-4)-β-D-glucan (lichenan) content was determined according to AOAC method 995.16 (McCleary and Codd 1991). Lichenans were degraded to glucose by using lichenase and β-glucosidase, and glucose was determined by spectrophotometry. However, initial experimentation showed that due to the high amounts of lichenan in some lichens, the amount of sample needed to be reduced to 25 mg. The boiling time with sodium phosphate buffer was also increased to 13 minutes to assure solubilisation of the sample. Total, soluble and insoluble dietary fiber were analyzed according to the enzymatic-gravimetric AOAC method 991.43 (Lee et al. 1992), but due to high fiber content and the problems of high viscosity during filtration, the amount of sample was reduced to 300 mg. The samples from Harangervidda were also analysed for monosaccharide composition of the fiber fraction. This analysis was conducted at the Norwegian Food Research Institute by gas-liquid chromatography according to the method of Englyst et al. (1992), with the modification that the enzymatic pre-treatment to digest starch was not performed.

For determination of the ruminal breakdown pattern, a 200 mg sample was weighed into 100 ml syringes in duplicate. Ruminal fluids (200 ml) from 3 rumen fistulated reindeer calves fed a lichen dominated diet were pooled, mixed, and strained through 4 layers of cheesecloth and added to preheated buffer (Menke and Steingass 1988) in a 1:3 ratio. This was done for each of the 3 runs performed during a 3 week period. Thirty ml of the ruminal fluid buffer solution was added to each syringe and kept at 38° C in an incubator. In vitro gas production of each lichen species, in addition to cellulose standard (Whatman No.1 filter paper) was measured according to the method described by Menke and Steingass (1988). Gas production was recorded after 1, 2, 3, 5, 7, 9, 13, 18, 24, 28, 32, 34, 38, 46, and 52 hours. Gas production was corrected for blank gas production; triplicates of buffered rumen without sample in each run. The syringes were shaken by hand twice in the first hour and then 4 times daily during the rest of the incubation. Lichens species from 1 site of Hardangervidda and 1 of Jotunheimen were used in the experiment. Ten days before start and throughout the experimental period the animals were offered 1,000g DM per day of a diet consisting of 50% *Cladina stellaris* and 50% *Cetraria islandica*. The kinetics of fermentation were fitted to the exponential equation; $p = a + b(1 - e^{-ct})$ according to Ørskov and McDonald (1979) and Blümmel and Ørskov (1993), where p represents gas production at time t, (a+b) the potential gas production, c the rate of production. The a value is the intercept of the curve whereas the b value represents the fermentation of insoluble but potentially fermentable fractions of the feed.

Statistical analysis was performed using the Statistical Analysis System (SAS 1987). In the analysis of variance, a factorial design with location (mountain area) and lichen species as factors were used for the lichens collected in both mountain areas and for the parameters analysed from both locations. For pair-wise comparisons, the Ryan-Einot-Gabriel-Welsh multiple F-test was used. For the in vitro gas production data, a factorial analysis of variance design with run and lichen species as factors were performed, followed by Duncan's Multiple range test (SAS 1987) when appropriate.

Table 1. Content of dry matter, ash, crude protein, starch, and fiber fractions in lichens¹.

	No. of obs	Dry matter	Ash	Crude protein	Starch	Crude fiber	ADF	NDF
----- (% of DM) -----								
<i>Cetraria nivalis</i>	6	91.2	1.3 ^a ± 0.25	2.0 ^c ± 0.19	0.2 ^c ± 0.09	1.0 ^c ± 0.19	1.6 ^{bc} ± 1.22	6.8 ^c ± 4.03
<i>Cetraria islandica</i>	6	92.2	0.3 ^d ± 0.09	2.5 ^b ± 0.13	0.6 ^a ± 0.18	1.1 ^c ± 0.34	1.7 ^{bc} ± 0.66	16.0 ^c ± 7.43
<i>Cladina stellaris</i>	6	91.7	0.6 ^{bc} ± 0.26	1.9 ^c ± 0.08	0.2 ^{bc} ± 0.02	11.8 ^b ± 2.90	1.6 ^{bc} ± 0.60	67.6 ^a ± 9.02
<i>Cladina arbuscula</i>	6	91.5	0.4 ^{cd} ± 0.01	2.7 ^b ± 0.17	0.2 ^{bc} ± 0.02	9.9 ^b ± 4.42	1.8 ^{bc} ± 0.71	72.7 ^a ± 4.76
<i>Cladina rangiferina</i>	6	92.3	0.3 ^d ± 0.05	2.5 ^b ± 0.07	0.3 ^{bc} ± 0.06	24.2 ^a ± 3.43	2.9 ^{ab} ± 1.75	70.3 ^a ± 3.27
<i>Stereocaulon paschale</i>	6	92.6	0.7 ^b ± 0.12	7.5 ^a ± 0.14	0.3 ^b ± 0.03	7.8 ^b ± 1.35	3.6 ^a ± 0.62	48.7 ^b ± 8.54
<i>Alectoria ochroleuca</i>	3	93.6	0.5 ^{bcd} ± 0.08	2.6 ^b ± 0.11	0.2 ^{bc} ± 0.01	0.6 ^c ± 0.31	1.0 ^c ± 0.39	5.8 ^c ± 1.32

^{abcd}Means within column without common superscripts are significantly (P < 0.05) different.

¹Values are means ± standard deviation.

Results

Lichens from the mountain area Jotunheimen contained in average 2.3, 1.3, 9.4, and 1.3% more of crude fiber, ADF, NDF and total dietary fiber, respectively, than lichens from Hardangervidda. However, a significant effect of location was only found for ADF (P < 0.05). The large difference between mountain areas in NDF content was in particular caused by *Cetraria* spp., where the NDF content in average was more than twice as high at Jotunheimen as at Hardangervidda.

All the samples contained more than 90% DM after air drying, but some variation existed between species (Table 1). Ash content varied significantly between species, with the ash content of *Cetraria nivalis* being more than twice the amount (P < 0.05) than for the other species (Table 1). Significant differences also occurred between the other species. *Stereocaulon paschale* had 3 times higher (P < 0.05) crude protein content than the other lichen species, while the crude protein content in *Cetraria nivalis* and *Cladina stellaris* was lower (P < 0.05) than for the other species. Starch content was below 0.5% in all samples except for samples from *Cetraria islandica*, which had an average starch content of 0.55%.

Crude fiber content in different lichen species varied between 1 and 24.2%, the content being higher (P < 0.05) in *Cladina* spp. and *Stereocaulon paschale* than in *Cetraria* and *Alectoria ochroleuca* (Table 1). In addition, *Cladina rangiferina* had a higher (P < 0.05) crude fiber content than any of the other lichen species. Only small differences in ADF content were observed between species, while NDF content varied greatly (Table 1). The NDF content was significantly higher in lichens of the *Cladina* genus than in the other lichen species, and *Stereocaulon paschale* had a significantly higher NDF content than *Cetraria* spp. and *Alectoria ochroleuca*.

The total dietary fiber percentage was

higher than 77 in all samples analysed, and relatively little variation was found within species (Table 2). However, dietary fiber content was higher (P < 0.05) in lichens of the *Cladina* genus than in *Cetraria islandica*, *Stereocaulon paschale*, and *Alectoria ochroleuca*, while the value for *Cetraria nivalis* was intermediate.

Table 2. Total dietary fiber content of lichens.

	No. of obs	Minimum	Maximum	Mean	Std. Dev.
----- (% of DM) -----					
<i>Cetraria nivalis</i>	6	84.70	93.7	88.68 ^b	3.278
<i>Cetraria islandica</i>	6	77.50	87.4	83.02 ^c	3.395
<i>Cladina stellaris</i>	6	88.00	93.60	91.12 ^{ab}	1.940
<i>Cladina arbuscula</i>	6	89.50	95.00	92.23 ^{ab}	1.793
<i>Cladina rangiferina</i>	6	90.50	95.00	93.10 ^a	1.614
<i>Stereocaulon paschale</i>	6	82.30	88.00	84.80 ^c	2.045
<i>Alectoria ochroleuca</i>	3	84.00	85.80	84.80 ^c	0.917

^{abc}Means within column without common superscripts are significantly (P < 0.05) different.

The solubility of the dietary fiber, measured as the amount of dietary fiber soluble in water at 60°C, varied greatly between species and genera (Table 3). While less than 5% of the dietary fiber was soluble in lichens of the *Cladina* genus, more than 50% of the fiber was soluble in *Cetraria islandica* and *Alectoria ochroleuca*. In *Cetraria nivalis*, 21 % of the dietary fiber was soluble. The soluble dietary fiber content was only slightly higher in *Stereocaulon paschale* than in lichens of the *Cladina* genus.

The analysis of lichenan content revealed that this fiber fraction was only

present in *Cetraria* spp. and *Alectoria ochroleuca* (Table 4). The content was higher (P < 0.05) in *Alectoria ochroleuca* than in *Cetraria* spp., and higher (P < 0.05) in *Cetraria islandica* than in *Cetraria nivalis*. Lichenan content varied little within species.

Table 3. Soluble dietary fiber content of lichens.

	No. of obs	Minimum	Maximum	Mean	Std. Dev.
----- (% of DM) -----					
<i>Cetraria nivalis</i>	6	14.00	23.90	18.70 ^c	3.927
<i>Cetraria islandica</i>	6	44.70	54.30	49.83 ^a	3.721
<i>Cladina stellaris</i>	6	0.00	1.90	1.10 ^e	0.876
<i>Cladina arbuscula</i>	6	0.60	3.80	2.87 ^{de}	1.219
<i>Cladina rangiferina</i>	6	0.00	4.10	1.87 ^{de}	1.546
<i>Stereocaulon paschale</i>	6	2.60	7.00	5.55 ^d	1.707
<i>Alectoria ochroleuca</i>	3	42.40	47.10	44.33 ^b	2.458

^{abcd}Means within column without common superscripts are significantly (P < 0.05) different

Table 4. Total mixed-linked (1-3)(1-4)(-D-glucan (lichenan) content of lichens.

	No. of obs	Minimum	Maximum	Mean	Std. Dev.
		----- (% of DM) -----			
<i>Cetraria nivalis</i>	6	16.48	18.14	17.31 ^c	0.606
<i>Cetraria islandica</i>	6	24.47	27.12	25.99 ^b	1.007
<i>Cladina stellaris</i>	6	0.03	0.10	0.07 ^d	0.022
<i>Cladina arbuscula</i>	6	0.03	0.30	0.12 ^d	0.097
<i>Cladina rangiferina</i>	6	0.03	0.17	0.08 ^d	0.049
<i>Stereocaulon paschale</i>	6	0.02	0.07	0.05 ^d	0.018
<i>Alectoria ochroleuca</i>	3	32.81	35.05	33.78 ^a	1.156

^{abcd}Means within column without common superscripts are significantly (P < 0.05) different.

Table 5. Monosaccharide content from the lichen fiber fraction (n=3).

	<i>Cetraria nivalis</i>	<i>Cetraria islandica</i>	<i>Cladina stellaris</i>	<i>Cladina arbuscula</i>	<i>Cladina rangiferina</i>	<i>Stereocaulon paschale</i>	<i>Alectoria ochroleuca</i>
	----- (% of DM) -----						
Rhamnose	0.3 ^e	0.6 ^b	0.5 ^c	0.4 ^{cd}	0.4 ^c	0.8 ^a	0.3 ^{de}
Fucose	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a
Arabinose	0.6 ^c	1.0 ^b	0.7 ^{bc}	0.8 ^{bc}	0.8 ^{bc}	1.6 ^a	0.8 ^{bc}
Xylose	0.2 ^a	0.5 ^a	0.4 ^a	0.4 ^a	0.4 ^a	0.5 ^a	0.2 ^a
Mannose	13.9 ^d	11.9 ^d	42.9 ^a	35.9 ^b	33.2 ^b	26.6 ^c	6.7 ^e
Galactose	14.7 ^c	10.4 ^d	18.2 ^b	26.7 ^a	17.6 ^b	17.6 ^b	5.9 ^e
Glucose	32.3 ^c	53.8 ^b	22.3 ^d	19.3 ^d	33.9 ^c	21.4 ^d	61.3 ^a
Uronic acid	2.7 ^a	0.3 ^c	0.0 ^d	0.1 ^d	0.1 ^d	0.1 ^d	0.7 ^b
Total content ¹	58.4 ^d	70.8 ^{ab}	76.6 ^a	75.3 ^{ab}	77.9 ^a	61.7 ^{cd}	68.4 ^{bc}

^{abcd}Means within a row without common superscripts are significantly (P < 0.05) different.

¹Calculated as anhydromonosaccharides to reflect the content as polysaccharides.

Table 6. Degradation characteristics (means ± standard deviation) calculated from in vitro gas production runs (n=3) of seven lichens species¹.

Species	a	B	c	(a+b)
<i>Alectoria ochroleuca</i>	-5.9 ± 0.8a	76.9 ± 3.0c	0.056 ± 0.0009a	71.0 ± 2.3c
<i>Cetraria islandica</i>	-5.6 ± 0.9a	80.2 ± 3.5bc	0.051 ± 0.0014ab	74.6 ± 2.5ab
<i>Cetraria nivalis</i>	-5.6 ± 1.3a	77.2 ± 3.0c	0.054 ± 0.0052b	71.6 ± 3.1bc
<i>Cladina arbuscula</i>	-8.2 ± 0.5b	85.4 ± 3.8a	0.042 ± 0.0041c	77.3 ± 3.6a
<i>Cladina rangiferina</i>	-7.5 ± 1.1b	84.5 ± 2.3a	0.042 ± 0.0031c	77.0 ± 1.6a
<i>Cladina stellaris</i>	-8.3 ± 0.9b	83.7 ± 1.9ab	0.045 ± 0.0031c	75.4 ± 1.7a
<i>Stereocaulon paschale</i>	-7.7 ± 1.3b	83.7 ± 3.2ab	0.044 ± 0.0049c	76.1 ± 3.5a

^{abcd}Means within column without common superscripts are significantly ± p < 0.05) different

¹The kinetics of fermentation were fitted to the exponential equation; p = a+b(1-e^{-ct}), where p represents gas production at time t, (a+b) the potential gas production, c the rate of production. The a value is the intercept of the curve whereas the b value represents the fermentation of insoluble but potentially fermentable fractions of the feed.

fiber fraction differed between species, particularly for mannose, galactose and glucose (Table 5). *Cladina* spp. contained significantly more mannose and galactose than *Cetraria* spp. and *Alectoria ochroleuca*, and *Cladina stellaris* and *Cladina arbuscula* contained significantly less glucose. *Alectoria ochroleuca* had the highest glucose content. Ninety percent of the fiber consisted of glucose in this species.

Some variation in gas production rate did occur between runs and between species at some incubation times, but no fixed ranking of runs and species were found. Pooled data shows that gas production rate was higher (P < 0.05) during the first 5 hours of incubation in *Cetraria nivalis*, *Cetraria islandica* and *Alectoria ochroleuca* than in the other species (Fig. 1). The rate peaked in all species at 13 hours and dropped rapidly thereafter (Fig.

1). Differences in gas production rate in the initial phase resulted in higher total gas production in *Cetraria islandica*, *Cetraria nivalis* and in *Alectoria ochroleuca* compared to *Cladina* spp. and *Stereocaulon paschale* the first 9 hours of incubation. Total gas production at end of incubation did vary between runs (P<0.05), but not between lichens species, nor areas. However, a significant interaction effect between run and species was found.

Based on degradation kinetics (Ørskov and McDonald 1979) the readily fermentable fraction (a intercept) and the slowly fermentable fraction (b) varied between species and runs but not between areas. No interaction between species and run was found. The mean readily fermentable fraction was higher (P < 0.05) in lichens of the *Cetraria* genus and in *Alectoria ochroleuca* than in the other

lichens species whereas the mean slowly fermentable fraction was higher (P < 0.05) in *Cladina* spp. and *Stereocaulon paschale* compared to *Cetraria nivalis* and *Alectoria ochroleuca* (Table 6). The rate of gas production (c) did not vary between runs or areas. The mean rate was higher (P < 0.05) in *Cetraria islandica*, *Cetraria nivalis*, and *Alectoria ochroleuca* than in the other lichens species (Table 6). Estimated potential gas production (a+b) did vary between species with highest values in *Cladina* spp. and *Stereocaulon paschale* compared to *Alectoria ochroleuca* and *Cetraria nivalis* (Table 6). No effect of run or area was found.

Discussion

The results of this study demonstrate that lichens mainly consist of different fiber fractions, and that large differences in fiber composition and solubility occurs between species and genera of lichen. These results also demonstrate the strong limitations of traditional fiber fractionation methods like crude fiber, NDF and ADF in determining fiber content of lichens, since only a small and variable fraction of the fiber was detected with these methods. The low crude fiber and ADF content is due to the strong detergents used, which solubilizes a large part of the fiber. These fiber fractions are also meant to reflect the content of strongly bound fibers. The NDF fraction, on the other hand, is meant to reflect a higher portion of the fibers. However, this method does not take into account the fraction of the fibers that is soluble in a neutral detergent. Thus, NDF strongly underestimates the fiber content of plant material with a high amount soluble fiber. To determine the total amount of carbohydrates that are not immediately available to the animal, more sophisticated methods like the dietary fiber analysis and the monosaccharide fractionation method are necessary. With these methods, soluble fibers are precipitated by addition of ethanol, and thus will not be lost in the supernatant. Although the fiber contents using monosaccharide fractionation on an average was between 30 and 15% lower than when the dietary fiber analysis was used, the monosaccharide fractionation still confirms that the dietary fiber analysis reflects fiber content better than other methods. The suitability of dietary fiber as a measurement of fiber content is also reflected in the low standard deviation for this analysis within species. The lower

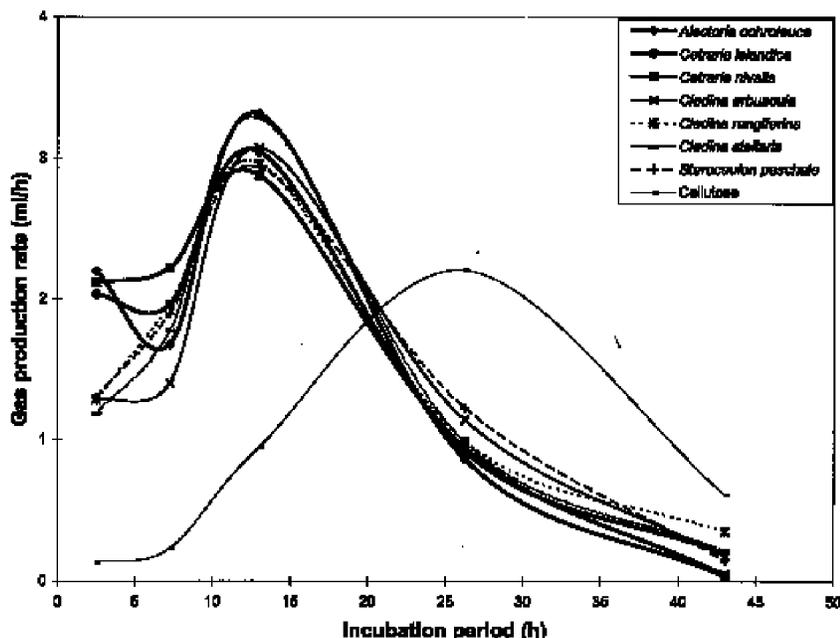


Fig. 1. Mean gas production rate of lichen species and cellulose at the following intervals: 0–5 hours, 5–9 hours, 9–18 hours, 18–34 hours and 34–52 hours through the incubation period.

value with the monosaccharide fractionation method could be due to losses that are known to occur during acid hydrolysis (Fincher and Stone 1986). The content of ash and crude protein and the content of 1.5 to 8.8% ether soluble substances as reported earlier (Garmo 1986, Presthegge 1954), also supports the values from the dietary fiber analysis, as these components constitute less than 12% of the lichen.

Garmo (1986) and Presthegge (1954), analysing the same lichen species, found at least twice as much ash as that found in our study. However, ash content varies with the extent of soil contamination in the samples. Protein content was comparable in these 3 studies. Garmo (1986) and Presthegge (1954) also reported much higher values (up to 4 times) for crude fiber than those obtained in this study. Solberg (1967), analysing 45 lichen species collected in Norway, also obtained much higher crude fiber values than those obtained in this study. The very fine grinding in our study (through 0.5 mm sieves) could be the cause of low crude fiber values, as the digested samples are filtered in the crude fiber analysis. However, the crude fiber content in these earlier studies were also much higher (4 to 6 times) in *Cladina* spp. than in *Cetraria* spp. and *Alectoria ochroleuca*, with *Stereocaulon* giving intermediate values.

Low values for ADF have also been reported before (Person et al. 1979, Danell et al. 1994). Person et al. (1979) reported ADF values of 4.6 and 3.7% in *Cladina*

stellaris and *Cetraria cucullata*, respectively. In the same study, the NDF content was found to be 83.0 and 31.6% for the same species. Thus, in the study of Person et al. (1979) the values from the Van Soest analysis were higher than in our study. Danell et al. (1994) also reported higher NDF values in *Cladina* spp. (76–78%) and *Stereocaulon paschale* (69%) than in our study. This may also be caused by a fine grinding in our study. However, *Cladina* spp. contained much more NDF than *Cetraria* spp. both in our and Person et al. (1979) studies. Very low values for starch confirm a general view that lichens do not contain starch.

The dietary fiber analysis indicates that the fiber content is greater in lichens of the genus *Cladina* than in the other genera investigated in this study. In addition to the variation caused by variation in fat, ash, and protein content as presented above, variations in fiber content between species could be explained by variable content of mono- and oligosaccharides and other low-molecular weight substances, like for example the lichen acids (Elix et al. 1984).

In all lichen species investigated in this study, mannose, galactose, and glucose were the major sugars present in polysaccharides. Hence, between 94 and 98% of the polysaccharides consisted of these hexoses. Solberg (1970) also concluded that lichen polysaccharides consisted of these monosaccharides. As our study demonstrated, glucose content may be present as lichenan. However, glucose may

also be present as isolichenan, which is an α -glucose present as polysaccharide through 1–3 and 1–4 bonds (Krämer et al. 1995). Another group of important polysaccharide in lichens is galactomannans. These polysaccharides generally consist of a backbone of mannose with galactose attached as side groups (Iacomini et al. 1985, Ingólfssdóttir et al. 1994). The content of mannose in relation to galactose in our study supports the conclusion that galactomannans are major polysaccharides, particularly in lichens of the genera *Cladina*.

The fermentability of different lichen species in the initial phase using rumen fluid (the first 10 hours) seems to be related to solubility values in the fiber analysis, as lichens with a high solubility of the fibers also had a high initial fermentation rate. Differences in solubility of the fibers could thus affect nutritive value of different lichens for reindeer. In this respect, lichens of the *Cladina* genus might be particularly challenging to digest, since these lichens contain very low levels of fibers that are soluble in water at 60°C.

The solubility and fermentability values obtained here also correspond to digestibility values obtained earlier. In a study by Garmo (1986), where rumen inoculum from sheep was used, the digestibility of dry matter was on an average 24% for *Cladina* spp. and 46 for *Cetraria* spp., while the values for *Alectoria ochroleuca* and *Stereocaulon* spp. were intermediate. Person et al. (1979), using rumen inoculum from reindeer and caribou, found similar values. Danell et al. (1994) reported in vitro organic matter digestibility (IVOMD) of *Cladina stellaris*, *Cladina arbuscula*, and *Cladina rangiferina* of 41, 57, and 69%, respectively. In vivo digestibility of organic matter in *Stereocaulon paschale* has been found to be 48.5 (Jacobsen 1981), while Danell et al. (1994) reported an IVOMD of 36% for the same species. Presthegge (1954) compared digestibility of *Cladina* spp. and *Cetraria* spp. in experiments with sheep. In this study, organic matter digestibility was on an average 48% for *Cladina* spp. and 74 for *Cetraria nivalis*. However, digestibility was only 48% for *Cetraria islandica*. The digestibility of *Cladina* spp. has been found to be greater in reindeer than in sheep. Jacobsen and Skjenneberg (1976) for example, found the digestibility of organic matter in reindeer to be 75%. No digestibility values for reindeer have to our knowledge been reported for the other lichen species.

Rumen turnover time is a critical para-

meter in order to evaluate the biological significance of this finding. White et al. (1987) reported a rumen turnover time of reindeer fed lichens of about 30 hours. This is surprisingly long compared to the rapid rumen breakdown of lichens, and may reflect the low food intake during winter in reindeer (White et al. 1987). The low intake in winter is probably a strategy ensuring acceptable energy intake and minimising protein losses since energy intake on a lichen based diet is positively correlated to nitrogen losses (McEwan and Whitehead 1970). The long turnover time and the fact that no differences in total gas production occurred between lichens at around 30 hours in our study may indicate that variation in solubility plays a minor role for the nutritive value of lichen species in winter.

During summer most of the energy extracted from green vegetation by the females are transferred to their offspring as milk (White and Luick 1984). In fall, milk production drops and the females may build up their fat reserves. Fattening implies high energy intake, and the only carbohydrate rich fodder with high digestibility available in late fall is lichens. Still some of the winter green vegetation is available with a protein content ensuring a positive protein balance. Because of the high intake, rumen turnover time will be rather short. Thus, during fattening in fall, a highly soluble fiber fraction that is rapidly fermented, may contribute to higher energy intake, since digestibility can be regarded as a product of 2 competing processes; digestion and passage rate (Van Soest 1994).

This may indicate a selective pressure towards preference of lichens high in soluble fiber, especially in late fall when intake is high and turnover time is short. In initial preference studies conducted in November and December offering 5 species of lichens, Holleman and Luick (1977) reported a consistent preference for *Cladina stellaris* and *Cladina rangiferina* compared to *Cetraria richardsonii*. However, before the trials the animals were fed a *Cladina* spp. dominated diet which may influence diet preference. Nordberg et al. (1995) found that reindeer preferred *Cladina* spp. compared to *Cetraria* spp. in cafeteria trials conducted in October. The possible nutritional advantage of highly water-soluble lichens is not manifested in these trials and it is known that reindeer/caribou selectively graze lichens of the genus *Cladina* (Ahti 1957, Karaev 1961, Ahti and Hepburn 1967). This indicates other driving forces

shaping the reindeer preference of lichens and may be connected to secondary compounds influencing nutrient balance.

It can be concluded from this study that although fiber was a major constituent in all lichens studied, the composition and solubility differed greatly among species and genera. These differences seem to be related to initial ruminal breakdown rate. Further studies are needed to investigate whether these differences in fiber composition and solubility may affect the nutritive value of the lichens for reindeer.

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Red deer and cattle diet composition in La Pampa, Argentina

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Abstract

Presence of 2 large herbivores in the same rangeland makes assessment of proper stocking rates and management practices rather complex. This study evaluated composition and overlap of red deer and cattle diets in a semiarid, temperate rangeland of La Pampa province, Argentina. Deer and cattle diets were estimated by microhistological analysis of feces. Fifteen samples were collected for cattle and deer during fall, winter, spring, and summer of 1994/95 (Period 1) and the same seasons of 1996/97 (Period 2). Red deer and cattle diets were different ($P < 0.01$) within each sampling season. Diets were also different ($P < 0.01$) among sampling seasons within each animal species. Red deer were better shrub users than cattle. Deer consumed more than 4 times the amount of shrubs than cattle during all seasons. Shrubs accounted for 28 to 50% of deer diets in most seasons, and from 6 to 12% in cattle diets. Forbs were a variable component of diets. However, red deer harvested more forbs than cattle in most sampling seasons ($P < 0.05$). Cattle were better grass users than red deer. Cows consumed more ($P < 0.05$) perennial graminoids in all seasons, and based their diet on cool-season perennial grasses. A trend for red deer to behave as an intermediate feeder, compared with cattle could be suggested. In the environment of our study, deer and cattle diet overlap varied greatly depending on availability of palatable fractions of forbs, shrubs, and grasses. Forb and shrub regrowth would reduce the diet overlap.

Key Words: Browsing, intermediate feeders, grass users, rangeland use, range diets, multi-species programs

Presence of 2 large herbivores in a confined native area makes assessment of proper stocking rates and management practices complex. Degree of diet overlap and conflicts of management for each animal species may result in lower productivity than expected. On the other hand, more than 1 large herbivore may better explore and use the plant community at several strata, and achieve greater productivity. Association and tolerance among animal species affect interactions and the way an ecosystem is utilized (Ellis et al. 1976). Diet overlap may not be detrimental to the rangeland if the range resource and its responses to grazing are understood (Vavra et al. 1989).

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Resumen

La presencia de 2 herbívoros grandes en el mismo pastizal complica la determinación de carga animal y la adecuación de las prácticas de manejo. Este estudio evaluó la composición y sobreposición de dietas de ciervo colorado y ganado bovino en un pastizal templado, semiárido de la provincia de La Pampa, Argentina. Las dietas de ambas especies fueron estimadas a través de análisis micro-histológico de heces. Quince muestras compuestas fueron recogidas por especie animal en otoño, invierno, primavera y verano de 1994/95 (Período 1) y también en las mismas estaciones de 1996/97 (Período 2). Las dietas de ciervo colorado y bovino fueron diferentes ($P < 0.001$) dentro de cada estación de muestreo. También fueron diferentes ($P < 0.01$) entre estaciones para cada especie animal. El ciervo hizo mayor uso del arbusto que el bovino. Consumió más que 4 veces la cantidad de arbustos que el vacuno en todas las estaciones. Esa clase vegetal aportó entre el 28 y el 50% de la dieta de los ciervos en la mayoría de las estaciones, y entre el 6 y el 12% de la dieta de los vacunos. La presencia de herbáceas anuales latifoliadas fue variable en las dietas de ambas especies, pero prevaleció en la de ciervo colorado ($P < 0.05$). Por su parte, el bovino hizo mayor uso de las gramíneas. El consumo de gramíneas perennes fue superior en bovinos. En particular, la clase correspondiente a gramíneas perennes invernales constituyó la base de su dieta a lo largo del año. En el ambiente de este estudio, las sobreposición de dietas dependió de la disponibilidad de fracciones palatables de arbustos, herbáceas latifoliadas y gramíneas. La presencia de herbáceas latifoliadas, y rebrote de arbustos redujo el grado de sobreposición. La información recogida sugiere un comportamiento ramoneador del ciervo colorado, comparado con el vacuno, en el pastizal pampeano.

Red deer (*Cervus elaphus*) were introduced to Argentina from Europe into the native environment of temperate and cold regions. Red deer populations increased and the species naturalized over the years. Current knowledge suggests that red deer have a high adaptable capacity to use available forage if diversity in the plant community is high (Kinuthia et al. 1992). The present study compares the botanical diet composition of red deer with cattle (*Bos taurus*) in a deer-fenced deer-cattle operation, based on rangeland of *caldén* (*Prosopis caldenia* Burkart) forest of Argentina.

Materials and Methods

Study Area

The study was conducted in the south-central region of La Pampa Province (Latitude 37° 30' S, Longitude 64° 8' W). Elevation ranges from 260 to 200 m from North-West (NW) to South-East (SE). The area receives an annual precipitation of about 519 ± 177 mm, with no snowfall (Roberto et al. 1994). Most precipitation falls in the spring and fall with the majority of forage growth occurring in these seasons. The landscape is defined by mesas and valleys running ordered from NW to SE, interspersed with sandy rolling hills. Soils are classified as Entic Haplustolls and Typic Ustipsamments, developed on sandstone, loess and limestone (Cano 1980). Discontinuous pretrocalcic horizons are present at varying depths, between 0.6 and 1-m deep (Cano 1980).

Vegetation and use

The area is a forest comprised of caldén (*Prosopis caldenia* Burkart), the dominant tree species. Under the tree canopy, there is a lower layer of woody species integrated by shrubs, including piquillín (*Condalia microphylla* Cavanilles), tramontana (*Ephedra triandra* Tul. em J. H. Hunziker), *Bredemeyera microphila* (Gris.) Hieron. ex Lorentz and Niederlein, pichana (*Cassia aphylla* Cavanilles), molle [*Schinus fasciculatus* (Griseb.) Johnston], llaollín (*Lycium chilense* Miers), piquillín de víbora (*Lysium gilliesianum* Miers), brusquilla [*Discaria longispina* (Hook. at Arn.) Miers], *Sphaeralcea crispera* Baker, tomillo [*Acantholippia seriphioides* (A. Gray) Moldenke], and mata trigo (*Baccharis gilliesii* A. Gray). The most conspicuous forb species are olivillo (*Hyalis argentea* Don. var. *Latisquama* Cabrera), peludilla (*Plantago patagonica* Jacquin), yerba de oveja (*Baccharis ulicina* Hooker et Arnot), trébol de carretilla [*Medicago minima* (L.) Grufberg], cardo ruso (*Salsola cali* Linné), *Rynchosia senna* Gill. Ex Hook. et Arn., *Nierenbergia aris-tata* (Sweet), revienta caballo (*Solanum eleagnifolium* Cavanilles), *Solanum chenopodium* (Cavanilles), *Triodanis biflora* (Ruiz et Pavón) Greene, quinoa (*Chenopodium album* Linné), and rama negra [*Conyza bonariensis* (L.) Cronquist] (Cano 1980).

Cool-season and warm-season perennial grasses comprise most of the of the forage supply in the region (Cano 1980). Fecilla negra [*Piptochaetium napostaense* (Speg.) Hackel] and fecilla fina (*Stipa*

tenuis Philippi) are the winter and spring dominant cool-season perennial grasses. Another perennial grass, unquillo (*Poa ligularis* Nees ex Steudel), is a companion species, highly palatable but less tolerant to grazing than the other 2. Overgrazed fields are dominated by the low-palatable cool-season perennial grasses such as paja blanca (*Stipa gynerioides* Philippi), paja fina (*Stipa tenuissima* Trinius) and pasto puna (*Stipa brachychaeta* Godron) (Cano 1980).

Important warm-season perennial grass species are pasto plateado (*Digitaria cali-formica* (Benth.) Henrard), penacho blanco [*Bothriochloa springfieldii* (Gould) Parodi], *Mulhenbergia gracillima* Torr., *Sporobolus cryptandrus* (Torr.) A. Gray, pasto fino [*Schismus barbatus* (L.) Thellung] and cola de zorro [*Setaria leucopila* (Scrib. et Merrill) Schumann]. Main cool-season annual grass species present in the area are cebadilla (*Bromus brevis* Nees), *Briza sub-aristata* (Lamarck), and centenillo (*Hordeum stenostachys* Godron). Relevant warm season annual grass species are paja voladora (*Panicum vergii* Arechavaleta), gramón [*Cynodon dactylon* (L.) Persoon], and roseta [*Cenchrus pauciflorus* Benth] (Cano 1980).

Cow-calf production is the region's main enterprise, based on yearlong native range use. The forest canopy increases in valleys and on side hills where soil depth is not as limiting as on mesas and hilltops. The more forested areas provide winter native range. Sandy areas and mesas are dominated by warm-season perennial grasses and are used as summer native range. Transition fields are used in different seasons as they suit production programs.

Study site

The study was conducted in a deer-fenced 2,500-ha ranch in the center of the mentioned area. Historically, the ranch maintained a cow-calf operation, and since 1990 a red deer program was included. The ranch has run 400 cows in the past. At present, it runs 350 cows and 300 red deer.

Sampling

Deer and cattle diets were estimated by identification of plant species and their relative proportions by microhistological analysis of fecal samples. Fifteen composite fecal samples were collected from cattle and red deer each season, during 2 sampling periods (1 and 2). Sampling seasons were defined as fall, winter, and spring of 1994 and summer of 1995 for Period 1, and the same seasons of 1996 and 1997 for Period 2. Collection seasons were established based on phenological

stages of dominant species (Cano 1980). Periods 1 and 2 were different in total rainfall and distribution (Table 1), which added climate variability. A wild fire in late summer of 1995 caused a temporary disturbance.

Individual samples were kept frozen and analyzed separately. Samples were thawed, oven dried at 50°C, and ground in a Wiley mill (1-mm screen). Samples were prepared for reading following the methodology described by Holechek et al. (1982) and botanical composition was estimated according to Sparks and Malechek (1968). Frequency of occurrence of each species in each sample was converted to relative density and used to calculate proportions in the diet (Holechek and Gross 1982). For analysis and discussion, species were grouped into plant species classes: cool-season perennial grasses, warm-season perennial grasses, shrubs, forbs, and annual grasses.

Statistical analysis

Data were subjected to analysis of variance with split-plot models including animal species in the main plot, and sampling season in the subplot. Multivariate analysis of variance for total diet comparisons between animal species by season within period was performed. Data of animal diets by plant classes or relevant individual plant species were submitted to analysis of variance (GLM, SAS 1985). Dietary overlap was estimated by period and season using the quantitative similarity index as described by Bray and Curtis (cited by Müeller-Dombois and Ellenberg 1974).

Results

Animal differences by season

Fall diets

Year of 1994 began with a dry summer. It was a dry year compared with 1996 (Table 1). Cool-season grasses delayed regrowth and annual forbs increased presence in diets. During fall of 1994, red deer fed on

Table 1. Seasonal precipitation (mm) during the years of study in semiarid South-central La Pampa, Argentina

	1994	1995	1996	1997
	----- (mm) -----			
Summer	173	249	654	179
Fall	101	67	109	
Winter	126	20.5	68	
Spring	141	185	423	
Annual total	541	521.5	954	

Table 2. Relative botanical composition (%) of red deer and beef cattle diets of a native range of South-central La Pampa^{1,2}.

Period 1	Fall	Winter	Spring	Summer
----- (%) -----				
Shrubs				
Cattle	3.7 ± 13.2	7.2 ± 6.67	3.8 ± 4.3	18.2 ± 6.7
Red deer	33 ± 10.2	38.7 ± 5.3	49.8 ± 4.3	41.8 ± 6.7
P ³	0.076	0.0034	0.0001	0.038
Cool-season perennial grasses				
Cattle	62.3 ± 4.8	73.0 ± 5.4	46.4 ± 1.6	41.0 ± 3.4
Red deer	2.6 ± 3.7	38.6 ± 4.3	4.2 ± 1.6	10.4 ± 3.4
P	0.002	0.0004	0.0001	0.0002
Warm-season perennial grasses				
Cattle	16 ± 3.8	4.4 ± 1.0	35 ± 3.8	36.8 ± 5.6
Red deer	6.8 ± 2.3	1.4 ± 0.8	31.6 ± 3.8	42 ± 5.6
P	0.09	0.04	0.55	0.53
Annual grasses				
Cattle	3 ± 0.5	1.4 ± 0.5	9.6 ± 1.1	0.2 ± 0.4
Red deer	1.2 ± 0.4	1.4 ± 0.4	7.6 ± 1.1	1.8 ± 0.4
P	0.04	0.97	0.22	0.02
Forbs				
Cattle	15 ± 13	14 ± 5.6	5.2 ± 1.4	3.8 ± 1.6
Red deer	56.4 ± 10	19.9 ± 4.4	6.8 ± 1.4	4 ± 1.6
P	0.02	0.42	0.44	0.93
Period 2	Fall	Winter	Spring	Summer
Shrubs				
Cattle	12.4 ± 4.2	2.8 ± 2.7	17 ± 4.2	4.8 ± 7.5
Red deer	42.4 ± 4.2	12.8 ± 2.7	29.4 ± 4.2	54.8 ± 7.5
P	0.001	0.031	0.07	0.0015
Cool-season perennial grasses				
Cattle	75.4 ± 3.3	88 ± 3.6	45.2 ± 4.7	58.6 ± 4.9
Red deer	41.6 ± 3.3	57.6 ± 3.6	20.2 ± 4.7	15.4 ± 4.9
P	0.0001	0.0003	0.006	0.0002
Warm-season perennial grasses				
Cattle	1.6 ± 0.4	3 ± 0.9	13.2 ± 3.4	26 ± 4.5
Red deer	0.6 ± 0.4	2 ± 0.9	36.8 ± 3.4	8.4 ± 4.5
P	0.11	0.46	0.0011	0.024
Annual grasses				
Cattle	0	1.0 ± 2.0	22.6 ± 3.4	1.4 ± 0.6
Red deer	0	18.2 ± 2.0	10.4 ± 3.4	0.4 ± 0.6
P	—	0.0003	0.04	0.24
Forbs				
Cattle	10.6 ± 2.3	5.2 ± 2.4	2.0 ± 1.9	9.2 ± 3.2
Red deer	15.4 ± 2.3	9.4 ± 2.4	3.2 ± 1.9	21 ± 3.2
P	0.17	0.25	0.68	0.03

¹Deer-fenced red deer and beef cattle 2,500-ha ranch was the study site. Botanical composition of diets was estimated from microhistological analysis on fecal samples of red deer (*Cervus elaphus*) and beef cattle (*Bos taurus*).

²Periods sampled: Period 1 = 1994/95; Period 2 = 1996/97. Season by animal species by plant species class interactions were detected ($P < 0.01$). Diet means are presented by plant species class and animal species within season and period.

³P = Probability value of $F < F_0$ for column means within plant species class.

shrubs and annual forbs, while cattle based their diet on perennial grasses (Table 2).

In 1994, shrubs and forbs made up for most of the red deer diet (88%), and about 20% of the cattle diet ($P = 0.01$). In fall of 1996, shrubs remained relevant in red deer diets, and forbs were present in much lower proportions (Table 2). No differences were detected ($P = 0.17$) between animal species. Proportions of cattle diets comprised by these 2 plant species were similar ($P > 0.45$) in fall of 1994 and 1996. *Condalia microphylla*, *Prosopis caldenia*, and *Ephedra triandra* were the major shrub constituents, *Conyza bonar-*

ensis and *Chenopodium album*, the major forb constituents of diets.

Perennial grasses accounted for less than 10% of the diet of red deer and up to 78% cattle diet in fall of 1994 (Table 2). Graminoid proportions increased to 42% in the deer diet, and comprised again most of the cattle diet (77%) in fall of 1996. This increment could have been associated with preceding environmental factors, such as greater summer and fall soil water in 1996, which resulted in early fall regrowth of cool-season perennial grasses. *Piptochaetium napostaense*, *Stipa tenuis*, *Poa ligularis*, and *Hordeum stenostachis*

were the major cool-season perennial grasses, and *Sporobolus cryptandrus* was the major warm-season perennial grass found in cattle diets during fall.

Annual grasses proportion in diets were twice as large ($P = 0.02$) in cattle compared with deer in fall of 1994. The reduced size of this fraction, however, made this class of negligible biological significance.

Winter diets

Proportion of shrubs were greater ($P = 0.003$) in deer diets than in cattle diets during winter of 1994. Shrubs accounted for about 40% of the deer diet and less than 10% of the cattle diet. *Condalia microphylla*, *Ephedra triandra*, *Lycium* sp, and *Prosopis caldenia* comprised most (92.5%) of the deer diet in this season. During winter of 1996, the proportion of grasses increased and the proportion of shrubs decreased in deer diets. Despite the decline, shrubs remained a relevant class in deer diets (Table 2).

Proportion of cool-season perennial grasses comprised a large fraction of deer and cattle diets in both winters (Table 2). Differences between the 2 animal species were evident ($P < 0.01$). This class accounted for most of cattle diets in both years, and sheared its importance with other classes in red deer diets. *Piptochaetium napostaense* and *Stipa tenuis* were the main grasses involved in winter diets of both animal species and periods. *Hordeum stenostachys* and *Stipa gynerioides* were especially relevant in cattle diets in winters of 1994 and 1996, respectively.

Proportions of warm-season perennial grasses in winter diets of cattle and deer in both periods were of little importance (Table 2). *Sporobolus cryptandrus*, *Muhlenbergia* sp., *Digitaria californica*, and *Setaria leucopila* were the main species of this plant class detected in winter diets.

Proportions of forbs were greater ($P < 0.01$) for winter of 1994 than for winter of 1996 in the diet of both animal species. Differences in proportions in the diet between deer and cattle were not detected ($P > 0.25$) for forbs in either period. *Baccharis gilliesii*, *Hyalis argentea*, *Plantago patagonica*, *Nierembergia aris-tata*, and *Baccharis ulicina* were the main forbs in winter diets of 1994, whereas, *Sphaeralcea crispa* was the main one in winter diets of 1996.

Proportions of annual grasses in winter diets were variable and year dependant. Proportions in diets were very low and similar ($P = 0.97$) between animal species in

winter of 1994. In contrast, proportions were greatly different ($P < 0.001$) in deer and cattle diets during winter of 1996. Cattle included very little of annual grasses in their diet during winter of 1996, while deer made of it an important class (Table 2). *Bromus brevis* was the major component of the annual grasses group in this season.

Spring diets

Proportions of shrubs were greatly different ($P = 0.01$) in diets of deer and cattle in spring of 1994. Shrubs accounted for half of the deer diet and a minor fraction of the cattle diet. (Table 2). Shrub proportions in the diet of red deer for spring of 1996 were lower than for spring of 1994. Conversely, shrub proportions in the diet of cattle were greater for spring of 1996 than for spring of 1994. Despite the decline, this plant class remained more important ($P = 0.07$) in the deer diet than in the cattle diet. *Prosopis caldenia* accounted for more than 85% of the shrubs consumed by deer in both springs. *Condalia microphylla*, *Ephedra triandra*, and *Lycium sp.* completed the remaining fraction. *Ephedra triandra* was the main shrub in cattle diets, followed by *Prosopis caldenia* and *Lycium sp.*

Proportions of cool-season perennial grasses were different ($P < 0.001$) between animal species in spring diets. This plant class comprised less than 5% of the red deer diet in spring of 1994 and 20% in spring of 1996. In contrast, cool-season perennial grasses comprised almost half of the cattle diets in both periods (Table 2). Spring diets of both animal species included *Stipa tenuis*, *Piptochaetium napostaense*, *Poa ligularis*, *Hordeum stenotachys* among the preferred plant species. Cattle diet included also regrowth of *Stypa gnerioides* in spring of 1996.

Proportions of warm-season perennial grasses in diets were similar ($P = 0.55$) between animal species in spring of 1994, and accounted for about 33% of the diets. In contrast, proportions of this class were greater ($P < 0.01$) in red deer than in cattle diets in spring of 1996. This reversed trend in selection of grasses for cattle and deer, could be explained by the high quality regrowth of warm-season perennial grasses in spring and the declining quality of other grasses. *Sporobolus cryptandrus*, *Digitaria californica*, and *Setaria leucopilula* were the most important species that comprised this class. Increased share of warm-season perennial grasses in the deer diets during the second period was coincident with increased proportion of *Digitaria californica*.

Proportions of forbs in diets of both ani-

mal species were low in spring. No differences between red deer and cattle diets were detected in the fraction accounted by forbs during spring of 1994 ($P = 0.44$) and spring of 1996 ($P = 0.68$).

Annual grasses were a minor fraction in diets of both animal species during spring. No differences were detected ($P = 0.22$) in this fraction between deer and cattle diets in spring of 1994, but differences were found ($P = 0.04$) in spring of 1996. Similar to the previous season, *Bromus brevis* comprised most of this plant class in this season.

Summer diets

Proportions of shrubs in deer diets were twice as large ($P < 0.01$) as in cattle diets in both summers. *Prosopis caldenia* accounted for 67% of the shrub fraction in the deer diet in summer of 1995. *Condalia microphylla* and *Prosopis caldenia* accounted for 48.5 and 25.9% of the shrub fraction consumed by deer in summer of 1997. The low proportion of shrubs in cattle diets in summer of 1997 would be consistent with a more humid year, compared with summer of 1995. An increased use of caldén pods by cattle and deer was identified in summer of 1995. Year 1995 was particularly dry compared with 1996 (Table 1) and, although not measured, caldén trees may have produced a more than normal amount of fruits.

Proportions of cool-season perennial grasses in the diet of cattle were about 4 times ($P < 0.01$) the proportion found in deer diets in both summers (Table 2). Cattle based about half of the summer diet on this forage class. These observations indicate that cattle maintained high consumption of cool-season perennial grasses during summer, whereas, deer declined use of this grasses class as they matured. *Piptochaetium napostaense* and *Stipa tenuis* constituted the main cool-season perennial grasses for red deer and cattle diets in summer of 1995. Both plant species comprised about equal proportions of their class in the diet of each animal species (42 and 40% in the deer diet; 37 and 35% in the cattle diet, respectively). Conversely, *Piptochaetium napostaense* comprised 98 and 94% of the class in red deer and cattle diets, in summer of 1997.

Proportions of warm-season perennial grasses were important in deer and cattle diets during summer of 1995, and no differences were detected ($P = 0.53$) between animal species. Relative importance of this class decreased during the summer of 1997 but differences between the 2 animal species were significant ($P < 0.05$). *Sporobolus cryptandrus*, was the main

component of the warm-season perennial grasses class in both summers.

Proportions of forbs were low and similar ($P = 0.93$) in diets of both animal species in summer of 1995. Forbs became more important in diets of summer of 1997. Differences ($P < 0.01$) between red deer and cattle diets in forb proportions were detected in this season. *Sphaeralcea crispera* was the major forb component of this class. Water availability may have been the largest contributing factor to a greater forb presence in diets during summer of 1997. Annual grasses had a negligible participation in summer diets of red deer and cattle in both periods.

Seasonal differences by animal species

Red deer based their diet on shrubs and forbs in fall (Table 2), over periods. During winter, consumption of cool-season perennial grasses by red deer increased when compared with fall consumption ($P < 0.01$), and the proportion of forbs declined ($P < 0.01$). In spring and summer, red deer based their diet on shrubs and the perennial graminoid classes. Warm-season perennial grasses level averaged 34 and 25% in the spring and summer diets, respectively. Annual grasses were relevant in spring diets of both periods and in winter of Period 2.

Cattle based their diet on perennial graminoids. Cool- and warm-season perennial grasses together comprised 70% or more of cattle diets in all seasons (Table 2). Forbs and shrubs were always present in cattle diets and were consumed as complementary forages, second to perennial grasses. Forbs were relevant in fall and winter diets over periods. Shrub class proportions in cattle diets were more important in spring and summer than in fall and winter (Table 2). Annual grasses showed an increased presence in spring of both periods sampled. Importance of this class in other seasons was low and year depending.

Diet overlap

Diet overlap between the 2 animal species varied with periods and seasons. Period 1 showed larger ($P < 0.05$) changes in diet overlap than Period 2. Low overlaps resulted in fall (14.2%) and spring (27.4%) of Period 1. Cool-season perennial grasses and forbs or shrubs were the main classes responsible for diet differences in fall. Cool-season perennial grasses and shrubs were the main classes responsible for diet differences in spring. Compared with fall and spring, overlap was greater ($P < 0.01$) in the other 2 sea-

sons (56.8 and 62.6% for winter and summer, respectively). In contrast with Period 1, Period 2 showed the greatest overlap in fall, which decreased ($p = 0.09$) progressively over winter and spring (56.8, 52.0, and 49.2%, respectively). Summer of 1996 showed the lowest overlap of this period with a significant drop to 33.8%, greatly different ($P < 0.01$) from the other 3 seasons. It appeared that a more humid year increased the importance of perennial grasses in deer diets during fall and spring. Still, shrubs comprised more than 50% of the deer diet in summer of 1997, whereas grasses comprised 84% of the cattle diet in the same season.

Discussion

Body size, anatomy, and ingestive-digestive physiology of each herbivorous species characterize the grazing strategy and define selectivity patterns (Schwartz and Ellis 1981). Body size of ruminants has a direct effect on forage selection. Larger herbivores are less selective than smaller ones. Total daily requirements of energy of large herbivores are greater and animals tend to harvest more fibrous diets (Schwartz and Ellis 1981, Gordon and Illius 1988, Illius and Gordon 1987, 1989). Smaller animals have faster metabolic rates, they have to eat higher quality foods than larger animals, but require less food. Narrow dental arcades correspond generally with high selection ability (Gordon and Illius 1988). In several animal species, combination of diet selection skills, moderate body size, and ease of movement add a competitive advantage to survival. Gordon and Iason (1989) placed red deer as an intermediate selector, between cattle and goat. These authors consider red deer to have lower capacity than cattle for digesting low quality forages, but a superior ability in browsing and grazing on good quality plant parts. Consequently, these different skills of herbivores change the potential use of plants and the nutritive value of diets.

Quantification of diets using microhistology of feces may be compromised by differential digestion of plant fractions and discernability limitations of fragments in fecal analysis. Although actual quantification of diets could have been biased in this study, cattle and red deer potential biases because of digestion should equal out. So, basic comparative conclusions would be valid (Vavra and Holechek 1980), and use of this tool generated information otherwise unfeasible. Red deer and cattle diets

differed throughout the year, given forage availability and plant species diversity with potential for browsing or grazing. Albeit interactions exist, a superior browsing activity for red deer, compared with cattle was shown. Across years, shrubs accounted for 28 to 50% of deer diets in most seasons, and from 6 to 12% in cattle diets. Red deer consumed more than 4 times the amount of shrubs observed for cows during all seasons. Relative importance of shrubs in the deer diets decreased in winter, when cool-season perennial grasses increased from fall season levels.

According to microhistology, proportions of forbs in diets were highly variable. Red deer consumed more forbs than cattle in most seasons ($P < 0.05$), however, no consistent trends could be defined. Forbs accounted for more than 50% of deer diet and 14% of the cattle diet ($P < 0.01$) in fall of 1994. Differences were also evident ($P < 0.01$) in summer diets. Although these effects are greatly circumstantial and year dependant, they suggest red deer exhibit a selection ability for highly palatable species. Importance of forbs in fall diets has also been reported by Kinuthia et al. (1992).

Cattle utilized more perennial grasses than red deer in all seasons, and based their diet on cool-season species. Cattle diets contained 3 times the amount of perennial grasses than deer diets in fall, spring and summer, and almost twice the amount in winter. Within the grasses classes, red deer seemed more selective than cattle. Differences between both animal species in relative proportions of major components within cool- and warm-season classes of perennial species, would suggest a greater selection of red deer for more palatable grasses. Similarly, Ellis et al. (1976) reported high sensitivity of deer to plant species, quality and phenological stage. Both animal species exerted a minor and complementary utilization of annual winter and summer grass, including *Bromus brevis*, *Hordeum stenostachys*, *Cynodon dactylon*, and *Digitaria californica*. The presence of these grasses is highly dependant on soil moisture conditions and the soil seed bank.

Research conducted in South-central Wyoming (Kinuthia et al. 1992) concluded that mule deer (*Odocoileus hemionus hemionus*) and pronghorn (*Antilocarpa americana*) behaved as browsers, and elk (*Cervus elaphus*), cattle (*Bos taurus*) and sheep (*Ovis aries*) as grazers. Results from our work would indicate that, in Argentinean central caldén forest, red deer behave as intermediate feeders or as graz-

ers depending upon presence of palatable species. A trend for red deer behaving as an intermediate feeder, compared with cattle could be suggested.

Observations showed also that deer and cattle diet overlap varies greatly depending diversity of forage on offer and availability of palatable fractions of forbs, shrubs, and grasses. Plant species diversity and presence of forb and shrub regrowth would reduce diet overlap in the environment of this study. A fairly diverse forage supply (trees, shrubs, forbs, and grasses) would allow red deer to collect a high-quality diet throughout the year. Browsing on trees and shrubs, added to the use of forbs and grasses during the growing period, would give red deer a strong competitive advantage. Similar results were obtained by Young (1938) and Kufeld (1973). Balmaceda and Digiuni (1983) described a similar browsing behavior for goats, differing from cattle, guanaco, and sheep. According to our results, introduction of red deer would increase browsing pressure on shrubs and low trees, which could result in a management tool for brush control. Similar roles of ungulates in shrub control strategies have been mentioned for goats in the literature (Olson and Hansen 1977, Hansen 1982, Kinuthia et al. 1992).

It is possible that certain environments could tolerate higher stocking rate with both, cattle and red deer, than with only one of them. Results would indicate that cattle and red deer could be integrated in production programs for the region without a large degree of competition. Management of red deer in deer-fenced operations with cow-calf programs will depend on the total carrying capacity based on grass production and the structure of the shrub population present. Management strategies for deer and cattle in this region, defined for cattle use, may overestimate grass utilization potential and underestimate quality required by red deer. On the other hand, underestimation of shrub offer and deer use of this plant species class may result in lower than optimal stocking. Fields with grass for cattle, few shrubs and trees could be classified as poor range for red deer. In contrast, fields with a less productive grass component, disturbed areas, and dense shrub mass may be better suited for red deer than for cattle. More research on compared feeding behavior, diet overlap and preferences under different stocking rates, and requirements of integrated systems is necessary to better define potential and limits of cattle and red deer production programs.

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Food aversion learning to eliminate cattle consumption of pine needles

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Abstract

Conditioned food aversions are a potentially useful tool to eliminate consumption of some toxic plants by livestock. This study examined consumption of pine needles (*Pinus ponderosa* Lawson) in South Dakota and Oregon by pregnant cattle. Averted cattle were conditioned to avoid green pine needles using a gastrointestinal emetic, lithium chloride; control (non-averted) animals were not treated. Averted and non-averted cattle were offered green pine needles during pen trials, and they were also grazed in pastures with abundant pine needles in 2 winter trials during 1997 and 1998. Averted cattle ate no green needles in pen trials in Oregon and South Dakota in either year; whereas, control cattle always ate some green needles during those tests. The 1997 South Dakota field trial was inconclusive: the averted cattle ate no needles and the control cattle ate almost no needles while grazing. In the 1998 Oregon field study, the averted cows began eating pine litter after 4 days in the pasture, and the aversion to green needles extinguished rapidly thereafter. In Oregon, controls ate more than 50% of their diet as pine needles, and particularly selected green needles from recently cut trees or branches. When the trial ended after 16 days, the controls and averted cattle were both eating about the same amount of green pine needles and dry needle litter even though they grazed in different pastures. Although averted to green needles, cattle did not appear to generalize the aversion from green needles to dry needle litter. Conditioning permanent aversions may require averting cattle to all forms of pine needles (i.e., green and dry) likely to be encountered in a pasture.

Key Words: diet selection, cattle diets, aversion, *Pinus ponderosa*

Conditioned food aversions are a potentially useful tool to eliminate consumption by livestock of some toxic plants, including tall larkspur (*Delphinium barbeyi* L. Huth., Lane et al. 1990, Ralphs 1997) and locoweed (*Oxytropis sericea* Nutt. in T. & G., Ralphs et al. 1997). In aversion trials, the animal is typically exposed once to a novel food to overcome neophobia. After the initial exposure, a gastrointestinal emetic (usually lithium chloride, LiCl) is given if the animal eats the target plant (Ralphs and Olsen 1990, Ralphs and Cheney 1993). The animal associates the resultant illness with the flavor of the plant and avoids eating the

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Resumen

La aversión condicionada a ciertos alimentos es una herramienta potencialmente útil para eliminar el consumo de algunas plantas tóxicas por el ganado. Este estudio examina el consumo de hojas de pino (*Ponderosa pine* Lawson) por el ganado gestante en las regiones de South Dakota y Oregon. Se condicionó ganado para evitar el consumo de hojas de pino utilizando emético gastrointestinal, cloruro de litio y se tuvieron animales control (sin tratamiento para inducir la aversión). A los animales con y sin aversión se les ofreció hojas verdes de pino en experimentos en corral y en dos experimentos conducidos en los inviernos de 1997 y 1998 estos animales apacentaron en potreros con abundancia de hojas de pino. En los experimentos de corral conducidos en Oregon y South Dakota el ganado con aversión no comió hojas verdes de pino mientras que el ganado sin aversión siempre comió algo de hojas verdes de pino. El estudio de campo de 1997 conducido en South Dakota no fue concluyente porque el ganado con aversión no comió hojas de pino y el ganado del grupo control casi no comió hojas de pino mientras apacentaba. En el estudio de Oregon de 1998, las vacas con aversión iniciaron a comer las hojas de pino del mantillo hasta después de 4 días de estar en el potrero y la aversión por las hojas verdes de pino desapareció rápidamente después de iniciar el consumo. En Oregon más del 50% de la dieta de las vacas control fue de hojas verdes de pino, particularmente seleccionadas de árboles o ramas recién cortadas. Al final del periodo de estudio (16 días), tanto el ganado condicionado con aversión como el control comían casi la misma cantidad de hojas verdes y secas de pino presentes en el mantillo, esto sucedió a pesar que ambos grupos apacentaban en diferentes potreros. Aunque el ganado se condicionó para rechazar las hojas verdes de pino, parece que esta aversión no se generalizó en el ganado para rechazar las hojas secas del mantillo. El condicionar el ganado para evitar el consumo de hojas de pino puede requerir que los animales se condicionen para evitar el consumo de todas las formas (verdes y secas) de hojas de pino que se pueden encontrar en el potrero.

plant in future encounters (Provenza et al. 1990). Ralphs (1997) determined that aversions created to keep cattle from eating tall larkspur lasted for at least 3 years if averted cattle were not grazed with non-averted cohorts.

Conditioned aversions are unlikely to be an all-encompassing solution for most livestock producers with poisonous plant losses for a variety of reasons (Ralphs and Provenza 1999). The conditioning procedure is labor- and time-intensive; nausea induced by the emetic is somewhat stressful for the animal; the aversion works best if animals are naive to the target plant, and it is more

difficult (but possible) to condition aversions to familiar plants; social facilitation will cause the aversion to extinguish if all herd animals are not averted; aversions to a specific plant may extinguish if averted animals eat closely related species. Solutions to poisonous plant problems will usually involve a number of other management options (e.g., tall larkspur; Pfister et al. 1999). Nonetheless, aversive conditioning may play an important preventative role in some ranching situations (Ralphs and Provenza 1999) and deserves careful consideration.

The purpose of this study was to determine if aversions could be conditioned in cattle to eliminate consumption of ponderosa pine (*Pinus ponderosa* Lawson) needles. Pine needles contain a diterpene acid that is a potent abortifacient compound (Gardner et al. 1994, 1996). Green and dry needles from the same source contain about the same levels of toxin (D. Gardner, unpublished data). When pregnant cattle consume pine needles (Pfister and Adams 1993, Pfister et al. 1998), abortions often occur and cows retain their fetal membranes (James et al. 1989). Calves may be born alive but often die shortly after birth. Pine needle-caused abortions and their sequelae of veterinary treatment and altered animal and range management costs the livestock industry millions of dollars annually (Lacey et al. 1988).

Methods

1997 Logan, Ut. Pen Trial

Ten Hereford x Angus pregnant cows (469 ± 16 kg body weight) were randomly divided into 2 treatment groups (n = 5): 1) controls, and 2) those averted to pine needles. They were each fed 9 kg day⁻¹ of alfalfa hay. Green pine needles were collected in South Dakota and frozen until use. Beginning in early January, 1997, all cows were fasted overnight and at 0800 hours offered 100 g of freshly-harvested green pine needles for 15 min each day. Cattle were offered needles for a total of 8 days in Logan. Control cows ate an average of 90 g day⁻¹ of needles during the final 6 days of conditioning in Logan. Based on previous work (Pfister et al. 1998), we determined that cattle in the averted treatment must eat a minimum of 20 g (i.e., 2 to 4 bites) in order to be adequately exposed to the "flavor" of pine needles. Those that ate > 20 g were dosed with lithium chloride (LiCl) at 200 mg kg⁻¹. The LiCl was mixed with tap water and given by stomach tube. Controls that ate needles were not dosed.

Three cows in the averted group ate 100 g of needles and were treated with LiCl on day 3. The fourth averted-group cow ate sufficient pine needles and was dosed for the first time with LiCl on the fifth day of exposure, whereas the fifth cow in the averted group never ate any pine needles and was not dosed. After the initial LiCl dose, each averted animal ate no needles in 2 subsequent pen tests in Logan.

1997 South Dakota Field and Pen Trial

The South Dakota pen and field tests were conducted on a commercial ranch near Pringle (43° 37' 44" N latitude, 103° 41' 47" W longitude, 1,538 m elevation) using the 10 cows conditioned in Logan. On the second day at the ranch (16 January 1997) the cattle were fasted overnight, then penned individually and offered 100 g of freshly-harvested pine needles for 15 min. Refusals were weighed to determine pine needle intake, and no LiCl was dosed. This test procedure was repeated periodically over the next 7 weeks. The next day the cattle were turned out to graze in 1 of 2 adjoining 3-ha pastures with abundant pine tree populations in the area described by Pfister et al. (1998). Dormant grasses such as western wheatgrass (*Agropyron smithii* Rydb.), sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and little bluestem [*Schizachyrium scoparium* (Michx.) Nash in Small] were abundant in the pastures. The averted and control cattle were not grazed in the same pasture for 14 days because we did not want consumption by control cows to influence the diet selection of cows in the averted group or vice versa (Ralphs and Olsen 1990, Ralphs 1997). The field study lasted 20 consecutive days, and the cattle were switched between pastures on days 5 and 10. On day 14 the dividing fence between the pastures was taken down and the 2 groups of cattle grazed together thereafter. Cattle grazed each day during daylight hours and were penned at dusk each night; each evening they were fed 2.5 kg cow⁻¹ of grass hay. Repetitive 5-min bite counts were conducted for each cow during all active grazing periods by rotating systematically through both groups of cattle (Pfister et al. 1998). During bite counts, we recorded bites of pine needles (green and dry litter), dormant grasses and shrubs. The field portion ended on 5 February 1997; cattle remained at the ranch until 8 March 1997 when they were retested in the pen for the final time.

1998 Logan, Ut. Pen Trial

Ten mature, pregnant beef Shorthorn cows (640 ± 46 kg) were randomly divided into 2 treatment groups (n = 5): 1) averted to green pine needles, and 2) untreated controls. Ponderosa pine needles were collected fresh from western Idaho and kept frozen until use. One hour before pine needles were offered at 0900 hours, cattle were given a preload consisting of 0.75% of their body weight of a ground concentrate/hay mix (60% alfalfa pellets [*Medicago sativa*]; 30% corn [*Zea mays*]; 10% soybean meal [*Glycine max*]). A second equal offering was also given at 1500; total feed offered slightly exceeded maintenance. On days when no pine needles were offered, cattle were given alfalfa hay ad libitum. After an overnight fast, cows were individually offered 100 g of green pine needles for 15 min beginning on 1 January 1998 (day 1). Eight of 10 cows (4 controls and 4 in the to-be-averted group) ate all 100 g on the first day of exposure, but none were dosed with LiCl. Intake by controls was highly variable on days 2 and 3 of exposure. During the remainder of the Logan pen trial from days 4 to 29, the 5 control cows were each offered 300 g, and they ate all the needles every day. On day 2 none of the cows in the to-be-averted group ate pine needles. On day 3 all 5 cows in the averted group ate 100 g of needles and were dosed with LiCl at 200 mg kg⁻¹ body weight immediately after eating needles. On day 6, the averted cows were again offered green needles and no needles were eaten. On day 8, the averted cows were retested, and 2 cows ate 50 to 100 g of needles and were again dosed with LiCl. The averted cows were retested weekly on days 13, 20, and 27, and all abstained until day 27, when the 3 averted cows that had not previously received a second LiCl dose ate 20 to 30 g of needles and were given a second dose of LiCl.

An extinction trial is the elimination of an aversion by repeated presentations of an unconditioned stimulus (i.e., flavor of target food) without negative feedback (i.e., LiCl-induced nausea; Garcia 1989). Since each pen test was an extinction trial unless cows ate needles and were dosed with LiCl, further pen studies in Logan were discontinued and all tests were conducted subsequently in a field study near John Day, Ore.

1998 Oregon Field and Pen Trial

The Oregon trial was conducted on a commercial ranch near John Day, Ore. (44° 15' 04" N latitude, 118° 54' 78" W longitude, 1,267 m elevation) for 16 days

(Jan. to Feb.) with the same cattle. Only 4 controls and 4 averted cattle were used as the other 2 cows were injured in an accident during transport and returned to Logan. An 18-ha pasture with numerous mature ponderosa pine trees was divided into 2 sections, and controls and averted cows grazed separately. The groups switched pastures every 4 days during the trial. Both green and dry needles were available; additional pine needles were provided by cutting down several trees within each pasture, and roughly equal amounts of freshly-cut branches from a nearby logging operation were deposited daily in each pasture. Each pasture had a 10- to 15-cm layer of dry needle litter under the intermittent tree canopy. Adequate amounts of dormant grasses (*Festuca idahoensis* Elmer, *Poa* spp., and *Bromus* spp.) provided virtually all of the available forage. Cattle were individually supplemented each evening with 1.8 kg of a ground mixture of corn (30%), alfalfa pellets (60%) and soybean meal (10%). Bite counts were performed as detailed above, except that we also recorded whether pine needles were eaten from live trees or from trees or branches that had been cut down. All cows were individually penned and offered 100 g of freshly-harvested green needles for 15 min on days 4 and 11 of the field trial.

Statistical analysis

Both pen and field trials for 1997 and 1998 were analyzed using a repeated measures model with treatment (i.e., averted and control), individual animals nested within treatment (error a), day, day x treatment and residual error (b). Means were separated using the LSD procedure of SAS (1988) after a significant ($P < 0.05$) F test.

Results and Discussion

Averted cattle ate no pine needles in the pen or field trials in South Dakota, whereas non-averted control cattle ate 45 g (SE = 10) of the 100 g offered in the various pen offerings. There was a day x treatment interaction in the pen trial as the control cattle ate 10 (SE = 8), 54 (SE = 17), 42 (SE = 15) and 74 (SE = 9) g of needles on the 4 dates that they were tested. This increase in amount eaten over time suggests that cattle learned to accept needles. In further pen studies with cattle eating pine needles, repeated exposure to needles has increased acceptance over time (Pfister unpublished data). Other studies have reported similar observations for ani-

mals response to novel foods (Launchbaugh et al. 1997). In the grazing portion in South Dakota, the control cattle ate only a few bites of pine needles during the 20-day trial, and they did not differ from the averted group (data not shown).

Even though the averted cattle ate no pine needles and controls ate needles in the pen trials, the South Dakota trial was inconclusive because control cattle ate almost no needles in the field test. In 2 previous trials at this location, cattle have either eaten a large amount of needles (~50% of bites), or very few, depending on the weather and snow depth (Pfister et al. 1998). During the first week of this trial, ambient temperatures were typical (i.e., well below freezing), but then the weather warmed to above normal temperatures. Probably the most important factor in the lack of field consumption was the lack of accumulation of snow; rarely did more than 6 to 8 cm of snow accumulate at one time during the trial. Past results have shown that snow depth and accessibility of forage are major factors in consumption of pine needles by cattle (Pfister and Adams 1993, Pfister et al. 1998).

The cattle used in the Oregon study readily accepted pine needles on the first exposure after an overnight fast, perhaps because of previous experience with terpene-laden browse on a sagebrush (*Artemisia* spp.)-dominated range. These cattle were naive to pine needles, however, and a key factor in conditioning strong food aversions is relative novelty of the food (Domjan 1980). Aversions to novel foods are easier to condition than are aversions to familiar foods (Ralphs and Provenza 1999). It is possible, but unlikely, that the 1-day exposure with no LiCl treatment weakened the aversion. Exposure to a flavor with no paired illness has weakened aversions in rats through a "learned safety" mechanism (Kalat and Rozin 1973). Nonetheless, Burritt and Provenza (1996) found that a 1-day exposure does not weaken aversions in sheep, and that 7 days of experience are required to undermine the subsequent aversion. The averted cattle required 2 LiCl-pine needle pairings to condition a complete aversion in the pen, but that is common in conditioning aversions in cattle (Ralphs and Provenza 1999).

In the Oregon field trial, there was a treatment x day interaction ($P < 0.05$) for amount of green needles (cut trees), pine litter, and grasses eaten (Fig. 1). The averted cattle took a few bites of green needles and litter on day 4 and, thereafter, increased the amount of litter eaten during

the next 7 days. Near the end of the trial on day 13, averted cattle began eating substantial amounts of green needles. The amount of grasses eaten diminished steadily during the trial in both groups of cows (Fig. 1) even though adequate grass was available in most of the pasture. On occasion the pastures were covered temporarily by snow, but generally temperatures were above normal, and it rained almost every day.

The averted cows ate no green pine needles in the first pen trial on day 4, whereas controls averaged 75 g cow⁻¹. In the last pen test on day 11, the averted cows again ate no green needles, and controls averaged 50 g cow⁻¹. We did not offer dry needles in any pen tests. One averted cow aborted her calf on day 13; the calf appeared to be fully developed but was born dead. This cow began eating pine litter on day 7 and ate mostly litter before aborting.

The aversion that had been conditioned to green needles was extinguished. Though untested, this may have been due to consumption of pine litter to which cattle were not averted. Initially, we observed that averted cattle avoided the dry needles even when eating grasses intermingled with substantial accumulations of dry needles. Indeed, the averted cattle actively spit out accidentally-ingested dry needles in those first few days. Nevertheless, after a few days, cattle began eating substantial quantities of dry needles, along with a few bites of green needles, and the aversion quickly extinguished. Two averted cows began eating needles first, followed by the remaining cows in the group. Social facilitation probably hastened the extinction of the aversion once some animals began to eat needles (Lane et al. 1990, Ralphs 1997). Aversions to locoweed and larkspur extinguish rapidly when grazing companions are eating the target plants (Ralphs and Provenza 1999).

Cattle were not averted to dry needles because I assumed they would generalize the aversion from the green needles to the dry needles. Apparently the flavor was sufficiently dissimilar that cattle were not deterred for more than a few days from consumption of dry needles. Olsen et al. (1989) reported that cattle averted to dry, ground larkspur did not generalize the aversion to fresh, green plant. In fact, Ralphs (unpublished) has recently found that cattle averted to 1 species of larkspur (*D. barbeyi*) using fresh plant do not generalize the aversion to another closely related larkspur species (*D. occidentale*) also offered as fresh material. It is difficult to speculate about similarity of flavors and how cattle might perceive dry and green

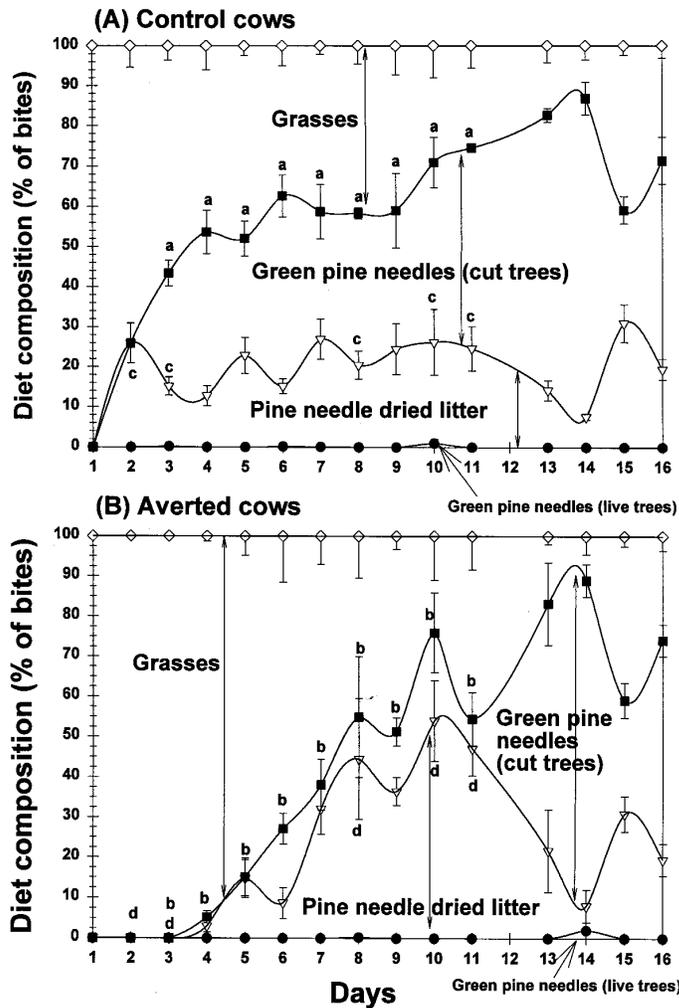


Fig. 1. Diet composition (cumulative percentage of bites with SE bars for each plant class) of control (i.e., untreated) and averted (i.e., conditioned to avoid pine needles) cattle near John Day, Ore. during late January and early February, 1998. Percentage composition is defined by the area between lines; for example for averted cows on day 1 grasses = 100% of bites, and on day 10 needles from cut trees = 22% of bites. For each particular day and plant class, different letters for controls and averted cattle indicate that diets differed ($P < 0.05$; a,b for green pine needles from cut trees; c,d for pine litter). Data for day 12 are missing.

needles. Intuitively, it seems that as overlap among flavors increases, generalization of an aversion will increase from one flavor to another. Losses of volatile compounds from green pine needles as they weather may result in flavors that are somewhat dissimilar. Further, weathered needles may initially be more acceptable to cattle than are fresh, green needles (Litvak and Monson 1998). Some toxic plants, like tall larkspur (*Delphinium barbeyi*), are not acceptable to cattle when immature (Pfister et al. 1997) but with changes in phenology become more acceptable, presumably because of flavor changes. These findings suggest that for aversions to be successfully created in grazing environments, livestock may need

to be averted to every potential form of the target plant that will be encountered.

Averted cattle retained the aversion created in a pen when retested in the field, even though the aversion was extinguished while grazing. This is similar to the findings of Ralphs and Olsen (1990) with regard to learning context. In their study, cattle that had extinguished an aversion to tall larkspur in the field retained the aversion when retested in a pen setting similar to that used in the original conditioning. Studies with rats (Lovibond et al. 1984, Bonardi et al. 1990) suggest that when a conditioned flavor (e.g., pine needles) is encountered in an unfamiliar context, the flavor is less capable of eliciting the same response (i.e., an aversion) than it does in

a familiar context. Burritt and Provenza (1997) suggested that livestock should be conditioned to avoid toxic plants in the environment where they will forage to increase the strength of the aversion, but this may be impractical under many ranching situations.

Control cows in the Oregon study ate large amounts of needles even though ambient temperatures were above normal during most days on the study site (average maximum daily temperature 6.1°C). This study cannot be realistically compared to other grazing studies that we have conducted on cattle eating pine needles (Pfister and Adams 1993, Pfister et al. 1998) because the control cows were conditioned to eat large quantities of needles in the pen, and this conditioning encouraged consumption of pine needles. Furthermore, cattle preferred the green needles from trees and branches that had been deliberately cut down over green needles from live trees. Anecdotal accounts suggest that cattle readily eat needles from slash piles, and this study confirmed that green, but drying, needles are readily accepted by cattle. Again, this may have been due to losses of volatile compounds from drying needles compared to needles on live trees (Litvak and Monson 1998). Thus, livestock producers with pine tree-infested pastures must exercise caution to keep pregnant cattle away from slash piles or fallen trees.

This study illustrates some of the potential problems with field application of aversive conditioning. First, the cattle used in Oregon had a history of eating browse, and this probably increased their propensity to eat pine needles. Second, the Oregon pastures were unfamiliar to all the cows, and the lack of familiarity may broadened diet selection patterns (Provenza 1997). Third, providing freshly-cut branches with green needles may have enhanced pine needle intake. Fourth, abundant dry needles mixed with grass may have provided the equivalent of multiple extinction trials as animals grazed in these patches underneath trees each day. Finally, it appears that cattle did not generalize the aversion from green to dry needles.

More work will be required to determine if aversive conditioning is a realistic option for livestock producers with toxicity problems from pine needle abortions. Cattle apparently must be averted to both dry and green needles in order to prevent consumption, and this reduces the practicality of the procedure. If pine litter is abundant, it may be difficult at times for cattle to avoid eating dry needles, thus

weakening the aversive conditioning. Once cattle begin to eat pine litter, aversions to green needles appear to extinguish rapidly.

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Fire history of the Rochelle Hills Thunder Basin National Grasslands

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Abstract

A fire scar chronology was constructed from ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) trees within the 70 km² Rochelle Hills Area of the Thunder Basin National Grasslands, in northeast Wyoming. A total of 65 fire scars occurred in 48 crossdated samples, and a master fire chronology was constructed for the period 1565 to 1988. No trees recorded more than 3 fires and most (26 of 42) recorded only one. For this reason, fire frequency intervals were considered as fire-free intervals in the Rochelle Hills Area. The Weibull Median Probability Interval (WMPI) for the entire period of record was 7.4; 7.9 for the non suppression period (1565 to 1939); and 6.7 for the suppression period (1940 to 1988). Infrequent occurrence of multiple scars, rough topography, and low potential substrates suggest that understory fuel loads were limited in amount and spatial consistency during most fire years. Position of scars within annual growth rings suggests that most fires (80%) occurred during the latter stages of the growing season or during the dormant period.

Key Words: fire intervals

Fire has been a significant disturbance process in terrestrial ecosystems since the origin of terrestrial vegetation, and lightning-caused fires have been responsible for shaping the structure and composition of most semiarid North American ecosystems (Wright and Bailey 1982). Native Americans used fire to manipulate ecosystems into seral stages favorable for human survival (Barret 1980, Fisher et al. 1987). With European settlement, however, fire suppression became a widespread practice throughout central and western North America, including the grassland ecosystems of northeast Wyoming.

Wendtland and Dodd (1990) concluded that pre-European settlement fire-return intervals ranged from 15–30 years within the area west of the confluence of the North and South Platte rivers to Fort Laramie Wyo., north to the Black Hills and south to the Kansas border, a northern mixed-grass prairie area similar to northeast Wyoming. Their research, based on a review of pioneer journals, diaries, letters, military records, eye witness accounts, and National Park Service fire records further indicated the fire-return interval has exceeded 50 years since 1935 within the

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Resumen

Se construyó una cronología de las cicatrices producidas por fuego en arboles de "Ponderosa pine" (*Pinus ponderosa* Dougl. & Laws) y "Rocky Mountain Juniper" (*Juniperus scopulorum* Sarg) localizados dentro del área de 70 km² de Rochelle Hills en el "Thunder Basin National Grassland" localizado al nordeste de Wyoming. Un total de 65 cicatrices se registraron en 40 muestras de diferentes fechas, y con ellas se construyó un cronología maestra del fuego ocurrido en el periodo de 1585 a 1988. Ningún árbol registró más de 3 fuegos y la mayoría (26 de 42) registraron solo uno. Por esta razón, en el área de Rochelle Hills, los intervalos de frecuencia fuego se consideraron como intervalos libres de fuego. El intervalo de probabilidad de la mediana de Weibull (WMPI) para el periodo completo fue de 7.4; 7.9 para el periodo de no supresión (1565 a 1939) y 6.7 para el periodo de supresión (1940 a 1988). La ocurrencia infrecuente de cicatrices múltiples, la topografía quebrada y los substratos potenciales bajos sugieren que las cargas de combustible de los estratos bajos fueron limitadas en cantidad y consistencia espacial durante la mayoría de los años de fuego. La posición de las cicatrices dentro de los anillos de crecimiento anual sugieren que la mayoría de los fuegos (80%) ocurrieron durante las últimas etapas de la estación de crecimiento o durante el periodo de dormancia.

boundaries of Scotts Bluff National Monument. They also determined that fire patch area has decreased, and that the timing of prescribed burns has shifted seasonality from characteristic late summer-early fall burns to late winter-early spring burns. Although much information has been garnered from historic journals, it is not as substantive as empirical evidence. However, very few sites exist within a grassland setting where physical evidence of fire can be obtained.

The Rochelle Hills Area of the Thunder Basin National Grasslands in northeast Wyoming contains relatively small pockets, within the grassland matrix, dominated by ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), both long-lived species that are known to form fire scars (Thilenius et al. 1995, Ahlefeldt et al. 1992). Fire histories have been developed for ponderosa pine communities in several regions throughout the western United States (Dieterich and Swetnam 1984, Fisher et al. 1987, Baisan and Swetnam 1990, Covington and Moore 1994, Brown and Hull-Sieg 1996). Although fire history research has been con-

ducted in neighboring ponderosa pine forests (the Black Hills area of Wyoming and South Dakota) (Fisher et al. 1987, Brown and Hull-Sieg 1996), the ponderosa pine areas of northeast Wyoming have not been investigated.

Our objectives were to: 1) determine fire frequency of the past few centuries; 2) determine if fire frequency has changed since the initiation of fire suppression; 3) determine seasonality of fire occurrence; and 4) assess fire location and size.

Study Area

The Rochelle Hills Area of the Thunder Basin National Grasslands covers approximately 70 km² in the Powder River Basin of northeastern Wyoming (Latitude 43° 32' 30"N, Longitude 105° 05' 00"W) (Fig. 1). Surface bedrock is sedimentary in origin and exposed rocks are Wasatch sandstone, Fort Union shale, and "scoria" or "clinker" formed from the baking of sandstones and shales by burning coal beneath the bedrock. Residual soils predominate on top of the escarpment and on steep slopes only a few centimeters of soil overlies bedrock. Rock outcrops are common on the steepest slopes (Breckenridge et al. 1974).

Mean annual precipitation is 31 cm (including snowfall precipitation equivalents), and mean annual snowfall is 114 cm. Precipitation occurs predominantly in

spring and early summer. The mean annual temperature is 8.1° C with 173 days of minimum temperatures below 32° C. Annual temperature extremes range from 43° C to -44° C (Martner 1986).

Trees are present in relatively narrow bands on the top and perimeter slopes of the Rochelle Hills escarpment. Three forest cover types occur in the Rochelle Hills (Thilenius et al. 1995). The Rocky Mountain juniper type occurs on steep, lower slopes at the base of the Rochelle Hills escarpment, and is most abundant on south and western aspects. Junipers grow in shrub form, and the understory vegetation is sparse, has little diversity, and provides little fine fuel production. The ponderosa pine/bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Schribn. & Smith) type occupies steep upper slopes and flat areas on top of the escarpment, and it is more prevalent in the eastern portion of the Rochelle Hills. Understory vegetation is more diverse and productive than in the Rocky Mountain juniper type, and Wyoming big sagebrush is present where the canopy is open. The ponderosa pine/Rocky Mountain juniper type is present on western and eastern slopes, but more common in the western portion of the Rochelle Hills and on northern aspects of small canyons. Herbaceous understory vegetation is almost absent and the ground surface is covered with conifer litter to a depth of 10 cm or more.

Large-scale fire suppression activities were initiated with the availability of sur-

plus World War II earth moving equipment and motorized vehicles with capacities to transport large amounts of water. Since approximately 1940, fires have been vigorously suppressed by government agencies and private land owners (J. Harshbarger, pers. comm.). We have taken 1940 as the dividing line between suppression and non-suppression periods in the Rochelle Hills.

Materials and Methods

All forested areas in the Rochelle Hills were surveyed for the presence of fire scarred trees. Scars containing charcoal were assumed to be of fire origin, scars without charcoal were treated as non-fire injuries. Live trees were sampled by employing a combination of methods outlined by McBride and Laven (1976) and Arno and Sneek (1977).

In the laboratory, samples were sanded sequentially with 60, 180, 320, and 400 grit sanding belts. Rings were examined with a 10 power stereo microscope to determine seasonality of fire occurrence by identifying scar location within the annual ring. Samples were crossdated to firmly establish fire occurrence years using standard dendrochronologic procedures (Stokes and Smiley 1968). A master fire chronology was then constructed for the entire area. Data analyses were performed using FHX2 Software (Grissino-Mayer 1995), and significance was determined at $P < 0.05$.

Kolmogorov-Smirnov Goodness-of-Fit Tests were performed on fire interval distributions to determine if a Weibull distribution (Hallinan 1993) modeled the interval data better than a normal distribution. Fire ecologists have suggested that fire interval data be modeled with a more flexible distribution than the standard normal distribution since fire interval data is often not normally distributed (Johnson and Van Wagner 1985, Johnson 1992, Baker 1992, and Grissino-Mayer 1995). The Weibull distribution is flexible enough to model both normal and negative exponential distributions (Hallinan 1993). Weibull distribution measures of central tendency are as follows: Weibull Median Probability Interval (WMPI); Weibull Fire Frequency Probability (1/WMPI) or the probability that a fire will occur in any given year; and Weibull Exceedance Probability Range (WEPR) or 95% confidence interval range. (For purposes of this report, the WMPI is used as a synonym for fire intervals). The difference between suppression

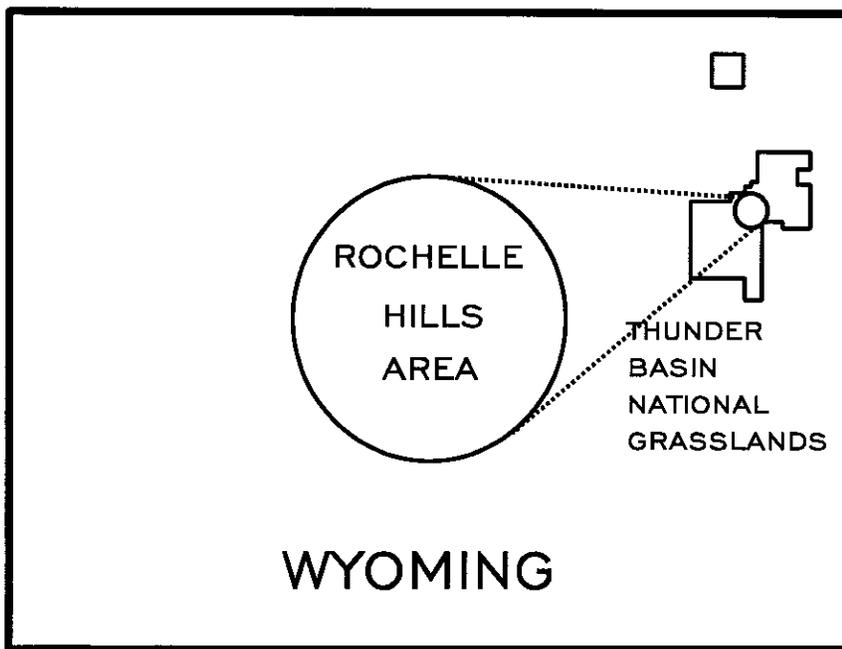


Fig. 1. Location of the Rochelle Hills Area.

and non-suppression fire interval means was determined by t-test. The FHX2 software transforms Weibull distributions into a data set that approximates the standard normal distribution, allowing the application of statistical tests such as the t-test which require normal distributions (Grissino-Mayer 1995).

A record of the seasonality of fire occurrence was compiled based on fire scar position within the annual rings. Baisan and Swetnam (1990) outlined the seasonal designations utilized: U = unknown, E = earlywood (a generic classification, where more precise identification is not possible), EE = early-earlywood (first 1/3 of earlywood), ME = middle-earlywood (second 1/3 of earlywood), LE = late-earlywood (last 1/3 of earlywood), L = latewood, and D = dormant (occurs between 2 rings, year of occurrence depends upon other scars of other trees to assign actual fire year). Each fire scar was examined to determine if the season could be identified. Seasonality summaries were based on fire years (year when a fire was recorded in the proxy record) rather than individual fires or scars.

Results

Fire History

A total of 65 fire scars were identified in 48 dateable samples from ponderosa pine (46 trees) and Rocky Mountain juniper trees (2 trees). These scars represent 42 different fire years between 1565 and 1988. Multiple scars were recorded on 16 trees. One tree recorded 3 scars and the rest recorded 2. A master fire chronology graph is displayed in Fig. 2.

Statistical analyses (Kolmogorov-Smirnov Test for Goodness-of-Fit) indicated non-normal distribution of the interval data and that a Weibull distribution modeled fire interval data adequately ($P = 0.41$). Central tendency measurements were therefore based on a Weibull distribution. Intervals reported here are fire-free intervals rather than fire-return intervals since trees exhibiting multiple scars were few. Romme (1980) and Wright and Bailey (1982) specify that fire-return interval refers to a point (i.e., a tree) or a very small stand, whereas fire-free interval refers to an area larger than a small stand. Mean fire-free interval is calculated using all fires that occurred in a given or specified amount of ground surface area, and the area size must be specified. In other words, the fire-free interval expresses the mean interval between all fires that

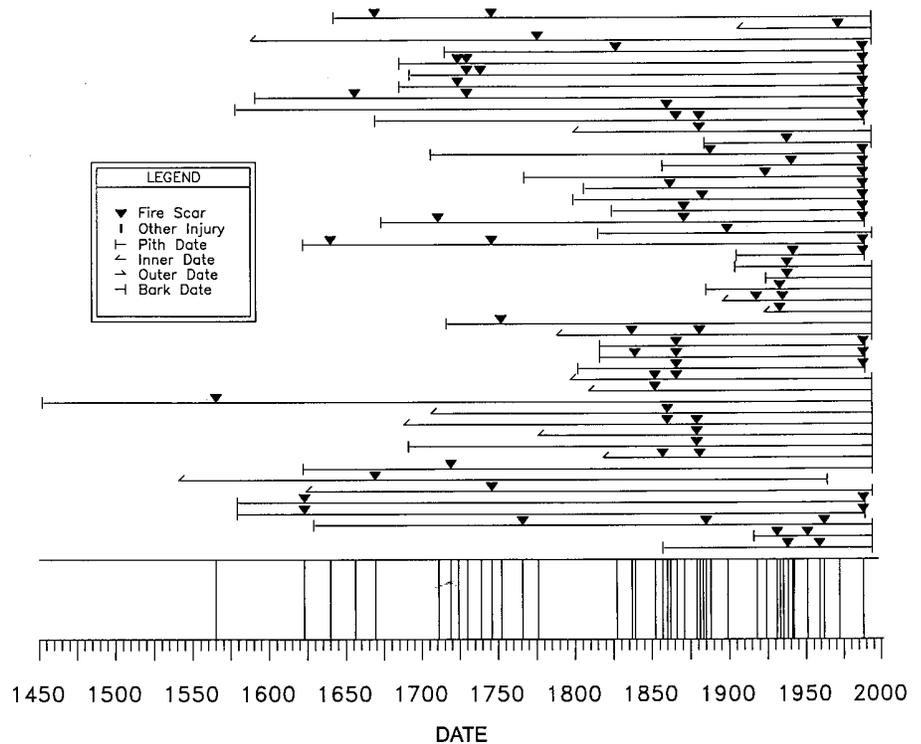


Fig. 2. Master fire chronology.

occurred during a period of record within a given area of land surface. The Rochelle Hills Area is the specified area in this case and covers approximately 70 km². The lack of multiple scars on single trees (points) mandates the use of fire-free intervals because, in this case where only 15 trees contained as many as 2 scars, a maximum of only 15 intervals would have been available to calculate the mean fire-return interval.

The Weibull Median Probability Interval (WMPI) of the entire period of record (1565 to 1988) is 7.4 ($n = 42$), with a Weibull Fire Frequency Probability (WFFP) of 0.14, and a Weibull Exceedance Probability Range (WEPR) of 1.1–22.0. The non suppression period (1565–1940) has a WMPI of 7.9 ($n = 34$), with WFFP of 0.13. The WEPR is 1.2 to 23.0. The suppression period (1940–1988) has a WMPI of 6.7 ($n = 8$), with a WFFP of 0.15 and WEPR of 1.0 to 21.0. There is no difference between the non-suppression and suppression period mean fire-free intervals ($P = 0.69$).

Within the non-suppression period composite chronology, the proxy evidence recorded several subperiods of alternating high fire frequencies and relatively long periods of no recorded fire years. Three long fire-free intervals occurred between 1566 and 1622, 1670 and 1710, and 1777 and 1826; that is 56, 40, and 49 years, respec-

tively. Each of these intervals is followed by a period of more frequent fire years.

Seasonality

Seasonality results (Table 1) are based on fire years (a year when a fire or fires occurred) rather than fire scars or individual fires. Basing seasonality on individual scars could introduce bias if a large number of trees were scarred by 1 or more fires during a particular year. The question we are concerned with is in what season(s) of the year have most fires occurred during the period of interest. We believe that using the fire year as a basis of comparison is appropriate in this type of forested system.

Late-season fires dominated the entire period of record. Fire years with late-season fires comprised 80% (31 of 39) of total fire years. During the non-suppression period, late-season fire years dominated. Combined late-early, late-, and dormant-season fire years comprised 84% (27 of 32) of the total fire years. Only 16% were early-season fire years.

The suppression period does not exhibit the same extreme late-season dominance. Only 57% of the fire years (4 of 7 total fire years) exhibited scars located in the late-early, late, and dormant-season annual ring positions. Sample size was very small for the suppression period, and may be skewing the inference. The scar record

Table 1. Summary of fire year seasonality

	Non-suppression period (1565 to 1940)	Suppression period (1940 to 1988)	Period of record (1565 to 1988)
Total number of scars recorded	59	8	67
Samples with identifiable season	56	7	63
Samples with undetermined season	3	1	4
Early-early season fire years	1	1	2
Middle-early season fire years	4	2	6
Combined Early Season (early-early and middle-early) fire years	5	3	8
Late-early season fire years	3	0	3
Late-season fire years	20	4	24
Dormant-season fire years	4	0	4
Combined Late-Season (late-early, late, and dormant season) fire years	27	4	31
Percent of total late-season fire years	84%	57%	80%
Percent of total early-season fire years	16%	43%	20%

showed no evidence of both early- and late-season fires occurring in the same year.

Fire location and size

Of the 42 fire years recorded during the period of record, 14 fire years were recorded by more than 1 tree, and 28 fire years were recorded by only 1 tree. This suggests that most of the recorded fires in this system were either small in area or were without the necessary heat required to scar trees. In either instance, understory fuel loads must have been generally low or discontinuous during most fire years.

The area producing the most scars from different fire years during the period of record was the eastern aspect (Fig. 3). There is a question whether this eastern portion of the Rochelle Hills actually burned more often because the topography is more prone to lightning strikes, or rather that the topography and fuel loads were more conducive for scar formation. We believe that the latter is correct. The understory vegetation characteristic of this portion of the study area was dominated by bluebunch wheatgrass and Wyoming big sagebrush (an indicator of high site potential for aboveground herbaceous biomass production). As a result, understory fuel production was probably more consistent, continuous, and volatile than other areas with lower site potential where the understory was dominated by Sandberg bluegrass (*Poa secunda* Presl., Rel. Haenk) and western yarrow (*Achillea lanulosa* Nutt.). Thilenius et al. (1995) indicated that this eastern portion of the study area, characterized by the ponderosa pine/bluebunch wheatgrass vegetation type, had the most well developed understory vegetation stratum in the study area. The grasslands to the east of the Rochelle

Hills also had a more level, unbroken topography, and the potential for more continuous fine fuel loads than the surrounding areas to the north, west, and south. For these reasons, we believe that the eastern portion of the Rochelle Hills has a greater potential for recording fire years in the proxy record.

Discussion and Conclusions

The mean fire-free intervals (WMPI) of both the non suppression and suppression periods (7.9 and 6.7, respectively) and the entire period of record, 1565 to 1988 (7.4), are consistent with mean fire-return intervals for other northern mixed-grass prairie areas located in the same geographic region. Wright and Bailey (1982) estimated a fire-return interval of approximately 5 years was probable in these grassland systems where topography was level or slightly rolling. Wendtland and Dodd (1990), based on pioneer journals, concluded that fire-return intervals in northern mixed-grass prairie areas (before 1935) were approximately 5 on smooth and gently rolling topography and 15 to 30 on more topographically diverse areas such as Scott's Bluff National Monument. Bragg (1985), using dendrochronology, calculated a mean fire-return interval of 3.5 before 1900, increasing to 8.5 between 1900 and 1958 in ponderosa pine areas of the Nebraska Sandhills. Brown and Hull-Sieg (1996) calculated the mean fire-return interval between 1668 and 1890 at Jewel Cave in the Black Hills to be 9 to 30. Shilts et al. (1980) estimated the fire return-interval in the grasslands of Wind Cave National Park to be 13 to 21 between 1820 and 1910. Between 1600 and 1770,

Fisher et al. (1987) estimated a mean fire-return interval of 27 decreasing to 14 between 1770 and 1900 at Devil's Tower National Monument.

There are at least 2 possible explanations for the low numbers of multiple scarred trees and for the majority of fire scars being recorded on only 1 or a few trees for any given fire year. Both are related to fine fuel characteristics. The first implies that fires were frequent, but were relatively small in spatial extent, resulting in only 1 or a few trees being scarred. A second explanation implies that fires were frequent, but possibly larger in spatial extent than in the first explanation. However, spatial discontinuities in the surface fuel load during most fire years, would have carried fires away from previously scarred trees. Both explanations would limit the opportunity for multiple scarring of individual trees and the scarring of trees in general. The second explanation seems more probable as many woodland communities in the north central plains are located where surface fuels are intermittent, discontinuous, and of such low quantity to retard fire spread and lower fire temperature reducing the number of trees scarred over an area and at specific points. This is consistent with the results of a similar study conducted by Brown of the Rocky Mountain Dendrochronology Lab (in prep, Feasibility study for fire history of the North Dakota Badlands: Final Report to Theodore Roosevelt Nature and History Association and Theodore Roosevelt National Park), in the Little Missouri Grasslands of North Dakota, an area very similar to the Rochelle Hills in substrates, topography, and vegetation communities.

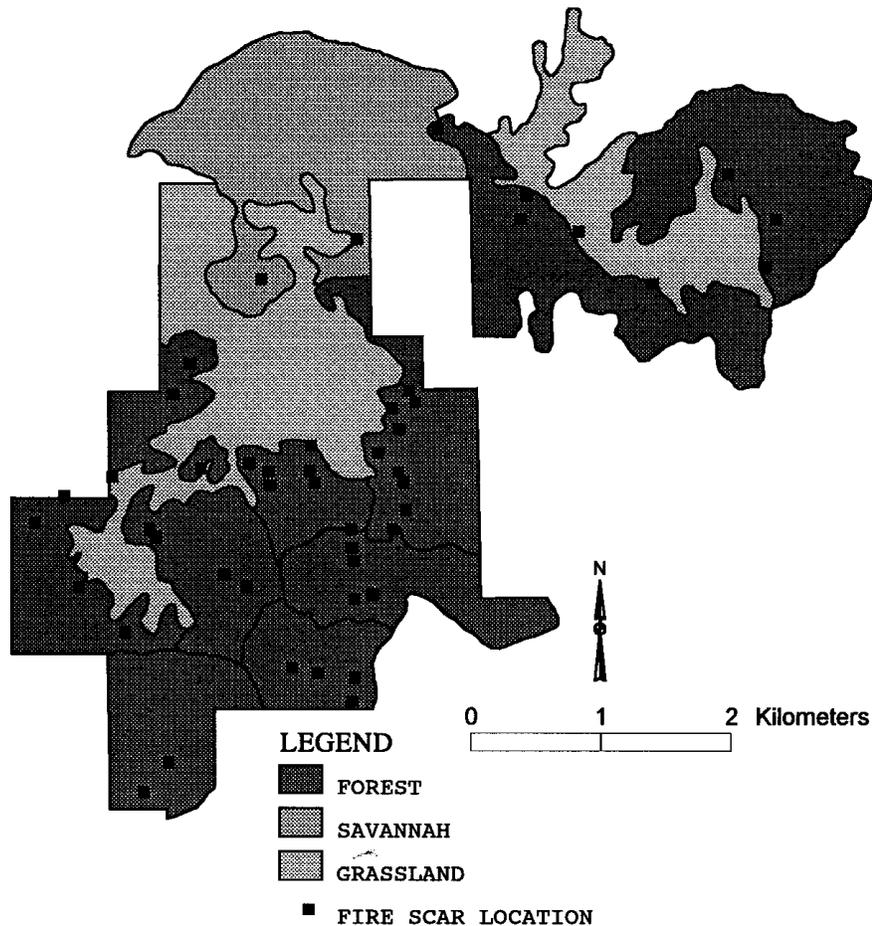


Fig. 3. Fire scar locations.

Thilenius et al. (1995) related that fire scars in the Rochelle Hills were not as common as encountered in ponderosa pine forests in the neighboring Black Hills. Surveying all tree areas for the presence of fire scars ensured confidence that the scar record sampled contained a high percentage of the fires recorded in the Rochelle Hills. Obviously, there is no guarantee that every scarred tree was sampled, or that all fires and fire years were recorded in the surviving proxy record. We therefore suggest that our estimates of fire-free intervals be considered as **minimum frequencies**. Sample depth is of some concern, particularly during the suppression period ($n = 8$). The sample depth during the non-suppression period ($n = 34$) may also be perceived as limited when compared to other fire frequency studies in ponderosa pine forests. As stated earlier, few opportunities exist within grassland settings where physical evidence of fire can be obtained. Tree-covered areas in this region are uncommon and relatively small, limiting the number of samples available for study.

More samples would be desirable, however they essentially do not exist. The addition of more samples that represent additional fire years would only reduce the calculated interval. If more samples could be obtained and our estimated intervals were reduced from approximately 7 to 5 or even 3, there would be little or no effect on any management plan or land use with respect to the interval. The addition of more samples that represent fire years already used in the calculation would not alter the intervals calculated here. Again we offer our estimates as minimum frequencies based on the sample depth available.

In the Rochelle Hills, the mean fire-free interval (WMPI) of the non-suppression period is not statistically different from the mean fire-free interval of the suppression period. Although suppression period sample size is limited, our estimates of minimum frequencies should limit the power (lowering the chance of not detecting a difference when there is a difference) that greater sample numbers (fire years) would generate. Also, there has been no major change in the road network and land use

(fire breaks), or the potential for fuel discontinuities in the Rochelle Hills that would suggest that fire would be less frequent during suppression times. Considering this, we believe that fire suppression efforts have had little or no effect on the fire-free interval of this system.

The large proportion of fires occurring late in the growing season during the non-suppression period is similar to results of both Wendtland and Dodd (1990) and Brown and Hull-Sieg (1996). The recent shift in fire occurrence from late season dominance to early season dominance observed by Wendtland and Dodd is similar to our observation. (However, spring season prescription burning has not been practiced in the Rochelle Hills Area, and our observations may be an artifact of low sample size.) Since spring prescription burning has not been employed, there is no reason to suggest that fire seasonality has changed since 1940. More accidental anthropomorphically generated fires may occur in the spring, but this is conjecture. These results also corroborate Higgins' (1984) conclusion that in northern plains grasslands, 73% of 294 lightning-ignited fires documented between 1940 and 1981 occurred during July and August.

An understory fuel load of sufficient spatial consistency and magnitude to carry a ground fire hot enough to scar trees is probably not present during most years in the Rochelle Hills. Although the fire-free interval has not changed since the initiation of suppression (circa 1940), the longer term effect of suppression is not yet clear. Prior to suppression efforts, fires were probably larger in spatial extent but scarring few trees. Fire size could now be smaller due to suppression. In both instances the potential for multiple scarring of trees would be limited. Suppression and subsequent increases in tree densities and litter accumulations which would normally be consumed by ground fires, could be setting the stage for more frequent stand replacing fires in forested areas. Most of the southern and southwestern forested areas of the Rochelle Hills currently have somewhat closed canopies, substantial amounts of litter accumulations, and relatively high tree densities. This set of circumstances will most likely lead to a future catastrophic fire, but it is unclear if fire suppression activities have given rise to this condition or if this condition is a part of the natural cycle in the ecology of this system.

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Tracked vehicle effects on vegetation and soil characteristics

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Abstract

A 3-year experiment to evaluate tracked vehicle effects on vegetation and soil characteristics was established on the Gilbert C. Grafton South State Military Reservation (CGS) in North Dakota. Study objectives were to evaluate the effects of 3 tracked vehicle use intensity treatments on plant species cover and frequency, and soil compaction. The 3 treatments evaluated include heavy use (74 passes), moderate use (37 passes) and no use. The moderate use treatment represents a typical use of 1 battalion unit at CGS with the heavy use treatment classified as 2 battalion units. This land area comprised a 50 by 150 meter block subdivided into three, 50 by 50 meter blocks. Each 50 by 50 meter block was subdivided into three, 16.7 by 50 meter blocks with each block treated with 1 of the 3 treatments. Soil bulk density increased ($P < 0.05$) on the moderate and heavy use treatments in the 0 to 15, 30 to 45, and 45 to 60 cm soil depths. Kentucky bluegrass (*Poa pratensis* L.) cover ($P < 0.05$) decreased in 1996 on both the moderate and heavy use treatments but was not ($P > 0.05$) different among all treatments in 1997. The tracked vehicle use on the heavy and moderate treatments did not change species composition or litter amounts after 2 years; however, bulk density and bare ground increased on both treatments in 1996 and 1997.

Key Words: Soil dry bulk density, plant community, personnel carrier, *Poa pratensis*, *Bromus inermis*

The acreage of army training lands is limited; therefore, care and maintenance of these lands is required to keep them viable for future training. The army's requirements for training lands have likewise increased, stressing the existing land bases. It is in the army's best interest to maintain the soils and vegetation on current training lands to sustain a realistic training environment. Without proper management, lands that receive intense use become devoid of vegetation and do not provide sufficient cover for troops and vehicles.

The National Environmental Policy Act of 1969 (NEPA) and Army Regulation 200–2 require that the Army minimize any significant short-term and long-term environmental impacts on natural resources (Goran et al. 1983). The army is responsible for maintaining ecological diversity and viability of the lands in its care. Furthermore, rare and endangered species, and the habitat

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Resumen

Se estableció un experimento de 3 años en la Reservación Militar Estatal Gilbert C. Grafon (CGS) de North Dakota para evaluar los efectos del paso de vehículos militares en la vegetación y suelo. Los objetivos del estudio fueron evaluar los efectos de 3 intensidades de paso de vehículos militares en la cobertura y frecuencia de especies vegetales y la compactación del suelo. Los 3 tratamientos evaluados fueron: uso alto (74 pasos), uso moderado (37 pasos) y sin uso. El uso moderado representa el uso típico de una unidad de batallón en el CGS y el tratamiento de uso alto representa el paso de dos unidades de batallón. El área experimental fue un bloque de 50 x 150 m dividido en tres bloques, cada bloque de 50 x 50 m se subdividido en 3 bloques de 16.7 x 50 m y en cada uno de estos bloques se aplicó uno de los tratamientos. La densidad aparente del suelo a las profundidades de 0–15, 30–45 y 45–60 cm aumentó ($P < 0.05$) en los tratamientos de uso moderado y alto. En 1996, la cobertura del zacate "Kentucky bluegrass" (*Poa pratensis* L.) disminuyó ($P < 0.05$) en los tratamientos de uso moderado y alto, pero en 1997 la cobertura de esta especie no difirió entre tratamientos ($P > 0.05$). Después de 2 años, el uso moderado y alto de vehículos militares no cambió la composición de especies ni la cantidad de mantillo; sin embargo, la densidad aparente y el suelo desnudo aumentó en ambos tratamientos en 1996 y 1997.

necessary to maintain those species on army land are protected by the Threatened and Endangered Species Act (U.S. Dept. of Interior 1973).

The study objective was to evaluate the ecological effects of tracked vehicle use on plant species cover and frequency, and soil compaction. The hypothesis was that tracked vehicle use on a Kentucky bluegrass-smooth brome (*Poa pratensis*-*Bromus inermis*) plant community in a transitional grassland would adversely affect soil dry bulk density and plant species composition. The results from this study will allow land managers and installation officials to understand the impacts that tracked vehicles have on the land base and adjust their training appropriately.

Materials and Methods

An experiment to evaluate the effects of an M113 full tracked personnel carrier on the vegetation plant community and soil characteristics was established in August 1995 in east-central North Dakota. Three tracked vehicle intensity treatments were evaluated including heavy use (74 passes), moderate use (37 passes), and no use (0 passes).



M113 personnel carrier.

The study site was on the Gilbert C. Grafton South State Military Reservation (CGS) near McHenry, N.D. (47°40'N, 98°40'W). This area is located in an area known as the Transition Grasslands (Küchler 1964, Whitman and Wali 1975, Barker and Whitman 1989). The study site occupied concave footslopes which receive additional runoff from upper slopes. This was evident by the buried soil horizons in the soil profiles. The soil series included Embden, Hecla, and Maddock with soils characterized as “coarse loamy” or “coarse silty”, mixed Pachic Udic Haploborolls. The vegetative plant community was classified as a Kentucky bluegrass/smooth brome grass (*Poa pratensis/Bromus inermis*) vegetative type dominated by Kentucky bluegrass (*Poa pratensis* L.) and smooth brome grass (*Bromus inermis* Leyss. subsp. *inermis*). Other major plants associated with the study site included western snowberry (*Symphoricarpos occidentalis* Hook.), yarrow (*Achillea millefolium* L.), white sage (*Artemisia ludoviciana* Nutt.), yellow sweetclover (*Melilotus officinalis* L.), heath aster (*Aster ericoides* L.), and soft goldenrod (*Solidago mollis* Bartl.).

Average annual precipitation (29-year average) at the McHenry weather station was 47.3 cm per year (NOAA 1995–1997). Annual precipitation was 63.2 cm, 47.5 cm, and 29.4 cm for 1995,

1996, and 1997, respectively. The 29-year average precipitation was 8.7 cm in June, 6.7 cm in July, and 6.9 cm in August. Precipitation was below the 29-year average for June and above the average for July for all 3 years. Precipitation was below the 29-year average for August with 5.5 cm, 3.1 cm, and 3.5 cm for 1995, 1996, and 1997, respectively. Data were collected in August and September for all 3 years of the study.

Tracked Vehicle Experiment

A M113 personnel carrier tracked vehicle was used in the experiment. This tracked vehicle has a flexible track driven by sprockets at the front of the vehicle. Consequently, the top and bottom rear portions of the track are under tension while the lower forward sections are relatively slack, thus, enabling the vehicle to traverse rough terrain. Rubber bushings provide torsional flexibility of the track segments which are 38 cm wide with a central rubber pad 15 cm wide. The M113 is equipped with 5 bogie wheels that are 71 cm on center, 1 drive socket and 1 idle sprocket. The length and width of the track are 305 and 38 cm, respectively. The gross full load weight of an M113 is 11,353 kg, exerting a ground pressure of 54.9 kPa (U.S. Dept. of Army 1990).

The one time application of a M113 personnel carrier was conducted on 2 differ-

ent use treatments on 7 August 1996. The moderate use treatment (37 passes) was derived from the typical use of 1 battalion unit at this military installation. The heavy use treatment (74 passes) was essentially doubling the rate of 1 battalion unit to see if any adverse effects would be observed. The control was considered a non use treatment (0 passes). A 50 by 150 meter tract of rangeland was selected by conducting a reconnaissance of the area in the summer of 1995 to select a typical landscape utilized by a battalion with tracked vehicles. This 50 by 150 meter tract of land was subdivided into three, 50 by 50 meter blocks of similar soil and vegetation to achieve 3 replicates. Each 50 by 50 meter block was subdivided into three, 16.7 by 50 meter plots with each plot treated with 1 of the 3 treatments using a randomized complete block design replicated 3 times.

Six soil cores were extracted from each treatment plot to determine soil dry bulk density as defined by Blake and Hartge (1986). Soil cores were collected from the center of the tracked vehicle lanes using a hydraulic coring machine (Giddings). A 7.5 cm metal core cylinder was fitted with a removable plastic sleeve which protected the sample during transport. The soil cores were taken at ground surface, minimizing compression of soil columns from within 3 dm (J. Richardson personal communication). Although this technique assured

Table 1. Soil particle size analysis for personnel carrier use treatments.

Treatment	Depth	Sand	Silt	Clay
	(cm)	(%)	(%)	(%)
Control	0-15	63.7	33.4	2.9
	15-30	61.2	35.3	3.5
Moderate	0-15	53.8	42.1	4.1
	15-30	51.3	44.8	3.9
Heavy	0-15	59.7	37.9	2.4
	15-30	57.5	39.7	2.8

minimal compression of samples at 3 dm, it is uncertain on the effects of the substrate below 3 dm. However, if a compression effect did occur it was equally represented among treatments. (J. Richardson, personal communication). The soil profile at each sampling site was classified and described. Soil cores were taken prior to and after application of the tracked vehicle use treatments in August 1996 allowing for comparisons of soil dry bulk density before and after each treatment. Soil water content was less than field capacity with soils characterized as instantly drained due to particle to particle contact (Wright and Sweeney 1977). Soils had water stable aggregates with excellent macroporosity in terms of soil structure due to high sands and bulk density levels 1 to 1.3 g cm⁻³. These were loosely compacted granular soils with high infiltration rates. Seasonal air temperatures were slightly below the long-term averages during this period. Soil cores were collected in August 1997 using the same procedures following a 1-year freeze-thaw cycle.

A 50 m transect was placed on 1 of the 2 tracked vehicle lanes by a randomly selected process for each treatment. Presence/absence of graminoid species were collected every 2.5 m along the transect using a 0.1 m² frame, while forb and shrub density was determined using a 0.25 m² frame. The 10-pin point frame was used to determine basal and litter cover as modified by Smith (1959) and described by Mueller-Dombois and Ellenberg (1974). Plant species data were collected in September 1996, four weeks after treatment to allow for plant recovery and again in August 1997 to determine effects 1 year after treatment to monitor compositional changes.

The study results are restricted to straight tracks. A single pivot turn has an immediate and obvious impact on vegetation by exposing bare ground, destroying native plants, and allowing primary succession plants to establish. The soils all had less than 5 percent clay content and were "coarse loamy" or "coarse silty"

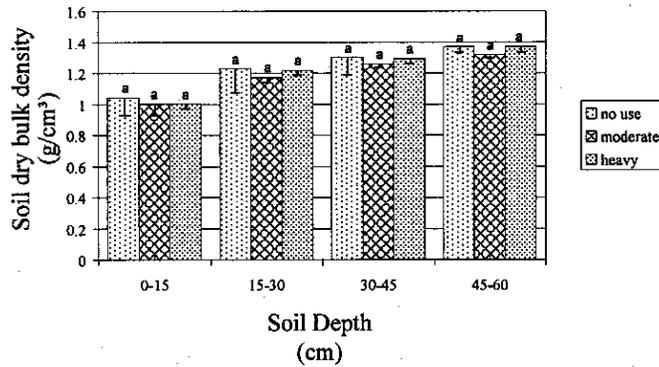


Fig. 1. Soil dry bulk density (g/cm³) prior to each tracked-vehicle use treatment in 1996. Within soil depths, treatments with the same letter are not significantly different (P > 0.05).

(Table 1). Although 3 soil series comprised the study site, no observed differences in soil composition were found between series. Attempts to select for only 1 series were thwarted due to the natural changes in soil profile components, short distances, and ablation till landscapes (M. Sweeney, personal communication).

Statistical Analysis

A one-way analysis of variance (ANOVA) was used to test for differences in soil dry bulk density among treatments (SPSS 1994). This procedure was used to determine differences using the graminoid presence/absence data, 10-pin point frame data, and forb and shrub composition data. Where significant differences were detected using a one-way ANOVA, a multiple comparisons test using the Tukey's procedure was carried out (Steel and Torrie 1980) with mean differences considered significant at the P < 0.05 level.

Results and Discussion

Soil dry bulk densities for each tracked vehicle use treatment (control, moderate,

heavy) were not different prior to treatment application in 1996, thus eliminating any site biases between treatments (Fig. 1). Soil dry bulk density did not differ between pre- and post-treatment on the moderate or heavy use treatments in 1996 (Figs. 2 and 3, respectively). However, the moderate and heavy use treatments had a greater soil bulk density at the 0 to 15, 30 to 45, and 45 to 60 cm depths when compared to the control following 1 year of treatment (Figs. 2 and 3). Soil dry bulk density increased with depth and tracked vehicle use, independent of number of vehicle passes when compared to the control. The exception was at the 15 to 30 cm depth where no differences were noted in either the moderate or heavy use treatment (Figs. 2 and 3). Similarly, Braunack (1986) and Wolf and Hadas (1984) found most change in soil dry bulk density occurred after pass, with subsequent passes having less effect. Braunack (1986) noted the area of disturbance, both in terms of depth and width of ruts, was greater with an increasing number of vehicle passes.

Subsoil compaction under heavy axle loads of military vehicles has been reported at depths > 50 cm (Gliemeroth 1948, Ericksson 1976, Voorhees et al. 1986).

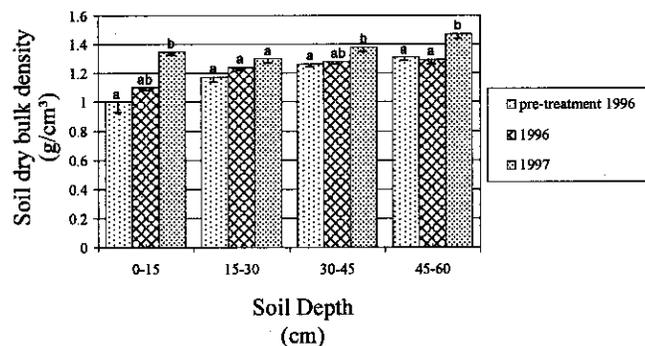


Fig. 2. Soil dry bulk density (g/cm³) on the moderate use treatment in 1996 and 1997. Within soil depths, time periods with the same letter are not significantly different (P > 0.05).

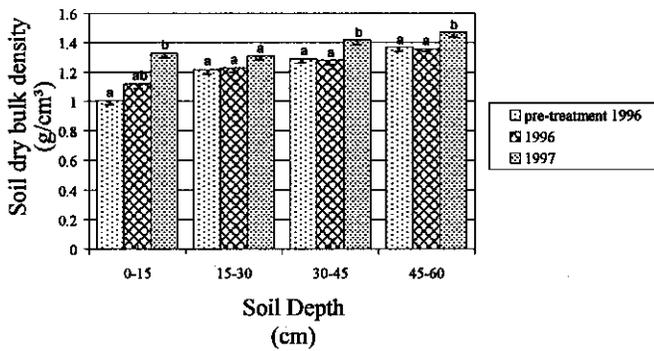


Fig. 3. Soil dry bulk density (g/cm^3) on the heavy use treatment in 1996 and 1997. Within soil depths, time periods with the same letter are not significantly different ($P > 0.05$).

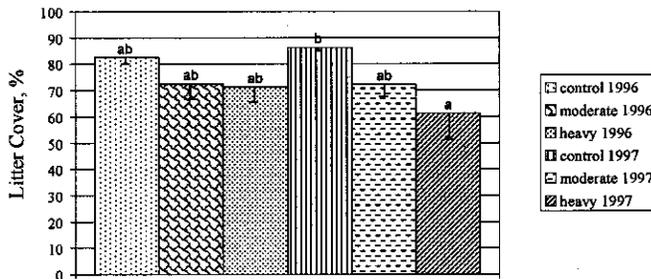


Fig. 4. Percent litter on treatment plots in 1996 and 1997. Treatments by year with the same letter are not significantly different ($P > 0.05$).

Our data would support their findings with subsoil compaction occurring from 0 to 15 cm and 30 to 60 cm under moderate and heavy use tracked vehicle treatments. However, no subsoil compaction occurred in the 15–30 cm layer differing from other studies previously reported. These studies reported soil compaction with high clay (>30%) content throughout the profile. Our study site had < 5% clay content with no over-consolidation or low K_{sat} due to high silt and sand content (Table 1). Soils with high sand and silt content do not express similar subsoil compaction characteristics as those soils having high clay content based on this study.

Litter cover on the control was 83 and 86 percent in 1996 and 1997, respectively (Fig. 4). Plant cover was 15 and 13% in 1996 and 1997, respectively. The moderate use treatment did not show any differences in percent litter composition in 1996 or 1997, or between years compared with the control (Fig. 4). Litter cover was reduced on the heavy use treatment compared to the control in 1997. Since the tracked vehicle in this experiment traveled straight lines (which is typical at CGS), litter present at the time of the experiment was not affected to any significant degree during year of application on the moderate use treatment. However, litter cover was reduced on the heavy use treatment 1 year following application.

Effect of tracked vehicle use on bare ground was different from the effects on litter. Total bare ground on the control was 2 and 1% in 1996 and 1997, respectively. Total bare ground increased to 19 and 18 percent on the moderate and heavy use treatments, respectively, following application in 1996. Bare ground remained greater on the heavy use treatment compared to the control, even 1 year following treatment, increasing to 25 percent on the heavy use treatment in 1997 (Fig. 5). Wilson (1988) found that Leopard tank use during May and June produced high frequencies of bare ground in native prairie, therefore encouraging invasion of introduced species at rates much higher than if driving occurred after 1 July. Wilson (1988) suggested that excluding

tank traffic during May and June would decrease damage to the native prairie, reduce opportunities for non-native plant species establishment, and increase the capacity of the vegetation to tolerate traffic at other times of the year. Based on Wilson's (1988) conclusion, this increase in bare ground could lead to an increase in non-native dicot plant species but should be minimal since the treatments occurred in August.

Kentucky bluegrass, classified as an alien species that is naturalized in the United States (Great Plains Flora Association 1986), decreased in basal cover on both tracked vehicle treatments following application in 1996. However, Kentucky bluegrass increased in basal cover by 74 and 126% on the moderate and heavy use treatments, respectively, and was no longer different from the control by 1997 (Fig. 6). Tracked vehicle use, independent of intensity, had a short-term negative impact on Kentucky bluegrass basal cover; however, recovered to pre-treatment levels after 1 year of application. Unlike Kentucky bluegrass, smooth brome grass basal cover did not change among treatments or between years in this trial (data not shown). It appears smooth brome grass recovered the high impact of tracked vehicle usage in the short term better than Kentucky bluegrass. However, after 1 year of post treatment, both graminoid species tolerated both levels of tracked vehicle use.

Forb and shrub species showed no negative effects from tracked vehicle use at either intensity level. Total density (stems 0.25m^2) of forb and shrub species did not change on either moderate or heavy use treatments between post-treatment levels and the control in 1996 or after 1 year of treatment application (Fig. 7). Since this site, as in most upland rangeland sites in the northern Great Plains Region, was graminoid dominant and forbs and shrubs a minor component (< 5 stems per 0.25m^2 and a confidence interval of 4.9 ± 5.2) of

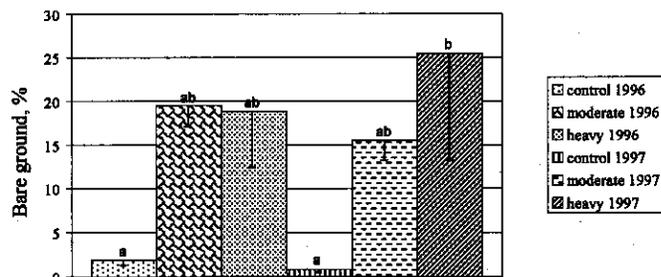


Fig. 5. Percent bare ground on treatment plots in 1996 and 1997. Treatments by year with the same letter are not significantly different ($P > 0.05$).

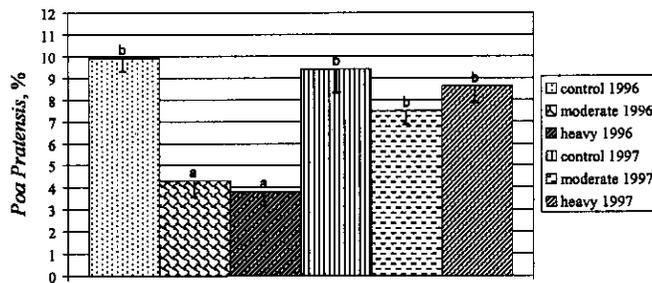


Fig. 6. Percent Kentucky bluegrass (*Poa pratensis*) cover on treatment plots in 1996 and 1997. Treatments by year with the same letter are not significantly different ($P > 0.05$).

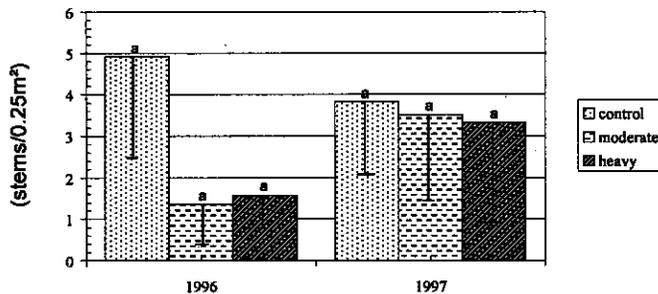


Fig. 7. Density (stems/0.25 m²) of forb and shrub species on treatment plots in 1996 and 1997. Treatments by year with the same letter are not significantly different ($P > 0.05$).

the plant community, determining effects on these plant types was non-conclusive.

Conclusion

Soil compaction must be alleviated if compaction has reached the point that root and plant growth and yields are impaired. Historically, soil freezing and thawing were assumed to eliminate compacted surface soil layers in most of the U.S. Corn Belt (Gill 1971) and that no special management was required. However, Voorhees et al. (1986) showed that subsoil compaction can persist for many years after the initial loading, in spite of annual freezing to the 90 cm depth. This study showed subsoil compaction persisted in the following year of tracked vehicle application, agreeing with Voorhees et al. (1986). One of the most direct methods for avoiding compaction is the concept of controlled traffic (Taylor 1983, Gerik et al. 1987). A controlled-traffic system restricts wheel traffic to specific lanes or inter rows. As a result, more of the soil area remains uncompacted than when a random or uncontrolled traffic pattern is used.

Our results indicated that 1 year of tracked vehicle use was not detrimental to the vegetation at CGS after 2 years of data collection. Although Kentucky bluegrass cover was reduced in year of tracked vehicle application, it showed no long-term

impacts in 1 year following treatment. Smooth bromegrass and dicot plants were not affected by moderate or heavy lane use of tracked vehicles in this study. There was no effect on litter cover and bare ground using the moderate tracked vehicle use treatment. However, litter cover was reduced and bare ground increased in the subsequent year following the heavy use tracked vehicle treatment. Soil dry bulk densities were significantly increased at the 0 to 15, 30 to 45, and 45 to 60 cm depths even after a freeze-thaw cycle had occurred, but appeared not to affect the vegetation.

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Book Review

An Introduction to Ecological Economics. By Robert Costanza, John Cumberland, Herman Daly, Robert Goodland, and Richard Norgaard. 1997. St. Lucie Press, Boca Raton, Florida. 275 p. US\$45.00 hardback. ISBN 1-884015-72-7.

Economists and ecologists now agree that the problems of desertification, habitat loss, and species extinction are global in scope. Further, researchers also concur that the solutions to these problems that have been proposed by scholars working within the confines of economics and ecology are not working because these solutions are, *inter alia*, narrow in scope. This recognition has led to a tremendous amount of interdisciplinary research between economists and ecologists (see the 1995 book *Biodiversity Loss: Economic and Ecological Issues* edited by C. Perrings et al. and the 1999 paper by A.A. Batabyal in Vol. 25, No. 4 of the *International Journal of Ecology and Environmental Sciences*). The purpose of this book is to give the reader a flavor of some of this research and to serve as a text "in introductory undergraduate or graduate courses, either alone or in combination with other texts" (p. xi).

Chapter 1 begins the proceedings by pointing out that innovative policies and management instruments are needed for 3 essential problems. These problems arise from the presence of (i) an unsustainably large and growing human population, (ii) entropy increasing technologies that deplete the earth of its resources, and (iii) land conversion that destroys habitat and increases soil erosion.

Although the authors do a good job of clearly discussing why these problems are salient, the clarity of this discussion is muddled by the presence of baffling sentences. Unfortunately, this is a recurring problem in this book. For instance, on p. 10 it is noted that "[e]conomists are almost unanimous in persisting in externalizing the costs of CO₂ emissions, even though by 1993 more than 180 nations had signed a treaty to internalize such costs." The authors should have provided some evidence to substantiate this claim. Certainly, this reviewer finds it difficult to believe that any reasonable economist would disagree with the proposition that there are external diseconomies associated with CO₂ emissions.

In Chapter 2, the authors discuss the historical development of economics and ecology. They point out that the "two disciplines differ markedly in that economics...is conceptually monolithic, while ecology consists of many competing and complementary conceptual frameworks" (p. 20). This chapter contains nice discussions of salience of the Second Law of Thermodynamics and the way in which we should be thinking about the right price for a given species or ecosystem. In addition to this, the authors rightly point out that one "of the strongest barriers to the union of economics and ecology has been the presumption that ecological and economics systems are separable and do not need to be understood together" (p. 64).

Despite these laudable aspects, once again, we are confronted with quixotic sentences. Here is an example. On p. 25, the authors say that "the economic model of society argues that individual behavior supports the common good while simultaneously arguing that communities are not needed because markets will provide for the common good." No citations are provided; as such, this reviewer is unclear as to which model the authors have in mind. However, if the idea is that communities are unimportant in mainstream economics, then this claim is, at best, misleading. One only has to peruse P. Dasgupta's 1996 paper in Vol. 1, No. 4 of *Environment and Development Economics* to get a sense for the salience of communities and communitarian solutions in mainstream resource and environmental economics.

The various problems and principles of ecological economics are examined in Chapter 3. For the most part, this is a well written chapter in which the authors make a number of significant points. At the outset, the authors cogently point out that the ecological economics vision consists of 4 basic points of consensus. First, the earth is a thermodynamically closed and non-materially growing system.

Second, our planet must be sustainable and ensure a high quality of life for all citizens. Third, the presence of fundamental uncertainty warrants a precautionary stance. Finally, our planet's institutions and management regimes should be proactive rather than reactive. Following this discussion, it is correctly noted that the "[i]nclusion of scale is the biggest difference between ecological economics and neoclassical economics" (p. 80). Finally, the chapter provides an engrossing account of the substitutability between different kinds of natural and manufactured capital. The upshot of this account "is that natural capital...and human-made capital are complements rather than substitutes" (p. 100).

Chapter 3 would be a truly fine chapter were it not for several errors of omission and commission. Here are 2 examples. First, the error of omission. On pp. 108–111, the authors discuss the population growth problem and some ways in which this problem might be ameliorated. Although it is now well known that female literacy plans a crucial role in determining the total fertility rate (see the 1997 book *Indian Development: Selected Regional Perspectives*, edited by Jean Dreze and Amartya Sen), strangely, the discussion of population control measures does not mention the fundamental role that female education plays in attenuating the population growth problem. Now, the error of commission. On p. 165, the authors contend that "[e]conomists systematically address the symptom of externalities but do not ask from whence externalities come." This is simply not true. As even a cursory perusal of standard resource and environmental economics texts will show, economists pay attention not only to the phenomenon of externalities but also to their causes. In fact, this dual attention has given rise to a sizeable literature on prices versus quantities.

The focus of Chapter 4 is on policies, institutions, and instruments. The authors first argue that the adoption of new technologies ought to be preceded by "the implementation of mass balance and energy balance accounting systems so that a comprehensive tracking of wastes is assured" (p. 189). They then note that in selecting stocks of environmental resources to be passed on to future generations, we should emphasize large-scale living ecosystems that are able to support evolutionary processes over sufficiently long time frames. Finally, it is pointed out that in order to achieve sustainability, it will be necessary to (i) enact a broad natural capital depletion tax, (ii) apply the precautionary polluter pays principle, and (iii) institute a system of ecological tariffs.

These are all worthwhile points and they deserve to have been made. However, the same cannot be said about some of the other points that are made in this chapter. Here is an example. On p. 217, the authors say that in "moving on from policy prescriptions to policy instruments for implementing policies, it is therefore not surprising to find economists in disagreement (e.g., pollution taxes vs tradable permits)...among themselves..." This sentence is certainly misleading. Before the work of M. Weitzman in 1974 (see Vol. 41 of the *Review of Economic Studies*), economists typically believed that price and quantity control instruments were equivalent in terms of their outcomes. As such, there was no need to disagree about these outcomes. Economists now (post-1974) know that under uncertainty, price and quantity control instruments can have dramatically different impacts. As such, depending on the curvatures of the relevant marginal benefit and cost functions and the nature of the uncertainty itself, different policy prescriptions are called for. Verily, this is a very different state of affairs from what the authors would have us believe.

In sum, this book is very much a mixed bag. It contains a number of bewildering and misleading sentences. However, the book also makes a number of useful points. In particular, it rightly points out that ecological and economic systems are jointly determined; as such, these systems ought to be studied together. Given this state of affairs, it seems appropriate to conclude by noting that most, but not all, of this book is worth your time.—Amitrajeet A. Batabyal, Rochester Institute of Technology, Rochester, New York.

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