Journal of Range Management

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Editor-In-Chief
SAMUEL W. ALBRECHT
445 Union Blvd., Ste 230
Lakewood, Colorado 80228
(303) 986-3309
Fax: (303) 986-3892
e-mail address:
sam_albrecht@ix.netcom.com

Editor/Copy Editor
GARY FRASIER/JO FRASIER
7820 Stag Hollow Road
Loveland, Colorado 80538
e-mail address:
gfrasier@lamar.colostate.edu

Production Editor
PATTY RICH
Society for Range Management
3059A Hwy 92
Hotchkiss, Colorado 81419-9548
e-mail address:
prich@starband.net

Book Review Editor
DAVID L. SCARNECCHIA
Dept of Natural Res. Sci.
Washington State University
Pullman, Washington 99164-6410
e-mail address:
scarneda@mail.wsu.edu

Electronic *JRM* Editor
M. KEITH OWENS
Texas A&M University
Research Center
1619 Garner Field Road
Ulvade, Texas
e-mail address:
m-owens@tamu.edu

Associate Editors
YUGUANG BAI
Dept. Plant Sciences
University of Saskatchewan
51 Campus Drive
Saskatoon, Saskatchewan
S7N 5A8
CANADA

ROBERT R. BLANK
USDA-ARS
920 Valley Road
Reno, Nevada 89512

KLAAS BROERSMA
Agriculture and Agri-Food Canada
3015 Ord Rd.
Kamloops, British Columbia
V2B 8A9 CANADA

JOE E. BRUMMER
Mt. Meadows Res. Ctr.
P.O. Box 598
Gunnison, Colorado 81230

DAVID GANSKOPP
USDA-ARS
HC-71 4.51 HWY 205
Burns, Oregon 97720

ROBERT GILLEN
USDA-ARS
Southern Plains Range Res. Sta.
2000 18th Street
Woodward, Oklahoma 73801

ELAINE E. GRINGS
USDA-ARS
Fort Keogh-LARRL
Route 1, Box 2021
Miles City, Montana 59301

MARSHALL HAFERKAMP
USDA-ARS
Fort Keogh-LARRL
Route 1, Box 2021
Miles City, Montana 59301

MITCHEL McCLARAN
University of Arizona
301 Biological Science East
Tucson, Arizona 85721-0001

PAUL OHLENBUSCH
Kansas State University
Department of Agronomy
Throckmorton Hall
Manhattan, Kansas 66506

ROBERT PEARCE
Resources Concept
340 N. Minnesota St.
Carson City, Nevada 89703

MICHAEL H. RALPHS
USDA-ARS
Poisonous Plant Lab
1150 E 1400 N
Logan, Utah 84341-2881

CAROLYN HULL SIEG
S.W. Science Complex
2500 South Pine Knoll
Flagstaff, Arizona 86001

FAISAL K. TAHA
Director of Technical Programs
Biosaline Agriculture Center
P.O. Box 14660
Dubai, U.A.E.

ALLEN TORELL
New Mexico State University
Agricultural Economics
Box 3169
Las Cruces, New Mexico 88003

MIMI WILLIAMS
USDA-ARS
22271 Chinsegut Hill Rd
Brooksville, Florida 34601-4672

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—to improve the effectiveness of range management to obtain from range resources the products and values necessary for man's welfare;

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Invited Synthesis Paper:
Principles and practices for managing rangeland invasive plants

ROBERT A. MASTERS AND ROGER L. SHELEY

Authors are field development biologist, Dow AgroSciences, 3618 South 75th Street, Lincoln, Nebr. 68506 and associate professor, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717. At the time this manuscript was submitted, Masters was rangeland scientist, USDA-ARS, 344 Keim Hall, University of Nebraska, Lincoln, Nebr. 68583.

Abstract

Invasive plants reduce the capacity of ecosystems to provide goods and services required by society, alter ecological processes, and can displace desirable species. They can reduce wildlife habitat quality, riparian area integrity, rangeland economic value, and enterprise net returns. The invasion process is regulated by characteristics of the invading plant and the community being invaded. The presence and spread of invasive plants is often symptomatic of underlying management problems that must be corrected before acceptable, long-term rangeland improvement can be achieved. Disturbance appears to be important early in the invasion process because it creates vacant niches that alien plants can occupy. Control of invasive plants may only open niches for establishment of other undesirable plants unless desirable plants are present to fill the vacated niches. In many instances, rangelands have deteriorated to the point that desirable species are either not present, or in such low abundance that plant community recovery is slow or will not occur without revegetation after invasive plants are controlled. Integrated weed management employs the planned, sequential use of multiple tactics (e.g. chemical, biological, cultural, and mechanical control measures) to improve ecosystem function (energy flow and nutrient cycling) and maintain invasive plant damage below economic levels, and emphasizes managing rangeland ecosystem functions to meet objectives rather than emphasizing a particular weed or control method. Sustainable, integrated invasive plant management strategies require assessing plant impacts, understanding and managing the processes influencing invasion, knowledge of invasive plant biology and ecology, and are based on ecological principles. Invasive plant management programs must be compatible with and integrated into overall rangeland resource management objectives and plans. Because of the complexity of managing invasive plants, it is imperative that relevant ecological and economic information be synthesized into user-friendly decision support systems.

Key Words: Biological control, herbicides, revegetation, native plants, alien plants, restoration, renovation, adaptive management, integrated weed management, noxious weed

Resumen

Las plantas invasoras reducen la capacidad del ecosistema para proveer los bienes y servicios requeridos por la sociedad, alteran los procesos ecológicos y pueden desplazar especies deseables. Ellas también pueden reducir la calidad del hábitat de la fauna silvestre, la integridad de las áreas ribereñas, el valor económico del pastizal y los retornos netos de la empresa. El proceso de invasión es regulado por las características de las plantas invasoras y la comunidad que esta siendo invadida. La presencia y dispersión de las plantas invasoras a menudo es un síntoma de problemas de manejo que deben ser corregidos antes de que se logren mejoras aceptables de largo plazo en el pastizal. El disturbio parece ser importante al inicio del proceso de invasión porque crea nichos vacantes que las plantas invasoras pueden ocupar. El control de plantas invasoras puede solo abrir nichos para el establecimiento de otras plantas indeseables, a menos de que estén presentes plantas deseables para llenar los nichos vacantes. En muchos casos los pastizales se han deteriorado al punto de que las especies deseables o no están presentes o están en una abundancia tan baja que la recuperación de la comunidad es lenta o no ocurrirá sin revegetación después de que las plantas invasoras han sido controladas. El manejo integrado de maleza emplea el uso secuencial planeado de tácticas múltiples (por ejemplo, medidas de control químico, biológico, cultural y mecánico) para mejorar la función del ecosistema (flujo de energía y reciclaje de nutrientes) y mantener el daño de las plantas invasoras abajo de niveles económicos, y enfatiza el manejo de la función del ecosistema de pastizal para cumplir con los objetivos en lugar de enfatizar en una maleza en particular o un método de control especifico.

Las estrategias sustentables del manejo integrado de plantas invasoras requieren de evaluar los impactos de las plantas, entender y manjar el proceso que influye en la invasión, el conocimiento de la ecología y biología de la planta invasora y son basados en principios ecológicos. Los programas de manejo de plantas invasoras deben ser compatibles e integrados dentro del plan y objetivos generales de manejo de los recursos del pastizal. Debido a la complejidad del manejo de las plantas invasoras es imperativo que la información ecológica y económica relevante sea sintetizada en sistemas de soporte de toma de decisiones amigables para el usuario.

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Invasive plants usually have many adverse impacts as they spread through terrestrial and aquatic ecosystems. In the seminal text, ***The Ecology of Invasions***, Elton (1958) described the impact of exotic or non-indigenous organisms invading new environments as "ecological explosions". Many of the estimated 5000 alien plants that now occur in natural ecosystems in the United States (Morse et al. 1995) were introduced for food, fiber, or ornamental purposes (U.S. Congress, Office of Technology Assessment 1993, Pimental et al. 2000). While many of these plants are of great value to agriculture, a small number have become invasive and threaten ecosystems.

Predicting which plants will be invasive and which ecosystems will be invaded is a highly desirable goal, but identification of salient characteristics of invasiveness and invasibility remains illusive (Crawley 1987, Mack 1989, 1996, Rejmanek and Robinson 1996, Wade 1997). Those plants that become invasive disrupt ecosystem processes and reduce the capacity of ecosystems to recover to a desirable state after disturbance and provide the goods and services (Costanza et al. 1997) demanded by society.

The presence and spread of invasive plants on rangeland is often symptomatic of underlying management problems that must be corrected before acceptable long-term progress toward control of the pests and rangeland improvement. Past rangeland management practices and climatic changes have contributed to plant community shifts by altering disturbance regimes that have accelerated invasive plant establishment and expansion (Hobbs 1989, 1991, 2000, Mack 1989, Hobbs and Huenneke 1992, Sutherst 2000).

The use of any single technology to control these species is usually not successful. Removing invasive plant species with chemical or biological control measures may only open niches for other undesirable species to occupy or to be reinvaded by the same species unless desirable species are present to fill the vacated niches. Where desirable species are either not present or in low abundance, plant community recovery will be slow or may not occur without revegetation (Masters et al. 1996, Masters and Nissen 1998).

Instead of relying on a single technology, integrated pest management emphasizes the sequential application of complimentary or synergistic control measures in an economically and ecologically effective manner (Pimentel 1982). Integrated pest management is the coordinated use of multiple tactics to assure stable ecosystem function and maintain pest damage below economic levels, while minimizing hazard to humans, animals, plants, and the environment (U.S. Congress, Office of Technology Assessment 1993). Integrated weed management emphasizes management of rangeland and pasture ecosystem function (energy flow and nutrient cycling) rather than a specific weed or control method (Scifres 1986). With this in mind, the goal of invasive plant management should be to reclaim or restore degraded weed-infested rangeland communities so that they are less susceptible to re-invasion by invasive plants and can meet land use objectives (Masters et al. 1996, Sheley et al. 1996).

Our purpose is to describe principles and practices to consider when developing integrated strategies to manage invasive plants on rangeland. Sustainable integrated invasive plant management strategies require assessing their impacts, understanding and managing the processes influencing invasion, knowledge of invasive plant biology and ecology, and integrating management tactics based on ecological principles. Ultimately, for these strategies to be successful, they must be compatible with and contribute to achieving overall rangeland ecosystem management goals and objectives.

Definitions

According to the Executive Order 13112 issued by the President of the United States on 3 February 1999, ***alien species*** are, with respect to a particular ecosystem, any species, including its propagules that is not native to that ecosystem. ***Invasive species*** are alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health. ***Native species*** are, with respect to a particular ecosystem, a species that, other than as a result of an introduction, historically occurred or currently occurs in that ecosystem. Cronk and Fuller (1995) considered an ***invasive plant*** as an alien plant spreading naturally (without the direct assistance of people) in natural or seminatural habitats, which produces a significant change in terms of composition, structure or ecosystem processes. A ***noxious weed*** is an undesirable plant species that is regulated in some way by law (Dewey and Torell 1991, Sheley and Petroff 1999).

Invasive Plant Impacts

Ecological

Ecological processes may change after invading species have established and spread (Walker and Smith 1997). These changes may be minimal and the plant invader may simply increase species richness. In contrast, where ecological processes are sufficiently disrupted, native species can be displaced, increasing plant community vulnerability to further invasion and regeneration of the invasive plant. When perturbation of ecosystems exceeds ecological thresholds, ecosystem change can be so profound that controlling the invader may not restore the ecosystem to a desired condition (Hobbs and Humphries 1995). Ecosystem processes, including hydrological cycles (Graf 1978, Loope and Sanchez 1988), erosion and stream sedimentation (Lacey et al. 1989), energy flow and nutrient cycling (Versfeld and van Wilgen 1986, Vitousek and Walker 1989, Stock and Allsopp 1992), native plant regeneration (Tyser and Key 1988, Woods 1993, Belcher and Wilson 1989, Kedzie-Webb et al. 2001), and fire regimes (Hobbs and Atkins 1988, Hughes et al. 1991, Whisenant 1990, D'Antonio and Vitousek 1992) can be altered by alien plant invasions. Cheatgrass (*Bromus tectorum* L.) invasion in the Intermountain West is thought to have been facilitated by overgrazing (Young and Longland 1996) or by cheatgrass' ability to occupy vacant niches and suppress native species recruitment on areas that have not been overgrazed (Svejcar and Tausch 1991). Cheatgrass proliferation has increased the frequency and intensity of fires occurring in sagebrush grasslands (D'Antonio and Vitousek 1992). This altered fire regime has reduced the abundance of native grasses and shrubs in these grasslands and enabled cheatgrass to dominate. Invasive plants also pose a threat to species designated as threatened or endangered by reducing the quality of natural areas established to protect habitats critical to the survival of these desirable species (Randall 1997).

Invasive plants can reduce wildlife habitat quality. Areas dominated by leafy spurge (*Euphorbia esula* L.) were used less by deer and bison than non-infested areas (Trammel and Butler 1995). On native bunchgrass sites, dense spotted knapweed (*Centaurea maculosa* Lam.) populations reduced winter forage available for elk in Montana (Thompson 1996). Elk use of spotted knapweed-infested areas increased 266% after spotted knapweed was controlled. In the Intermountain West, changes in fire frequency caused by cheatgrass invasions reduced native shrubs that are important for wildlife habitat (Miller et al. 1994).

Riparian areas are some of the most productive range sites in the West, with greater diversity of plant and wildlife species than adjoining lands (Sheley et al. 1995). In healthy riparian systems, vegetation removes sediment from water before it moves into streams. Riparian vegetation absorbs and dissipates the energy of floodwaters, thereby reducing streambank erosion. It also provides critical habitat for terrestrial and aquatic wildlife. Saltcedar (*Tamarisk* spp.), which has invaded wetlands and riparian streams throughout the western United States, reduces diversity and productivity of the herbaceous understory, and uses large quantities of water (DiTomaso 1998). Dense populations of saltcedar lower water tables, reduce surface water, decrease native vegetation needed by wildlife, and alter frequency of floods.

Economic

Economic impacts of invasive plants on rangeland have received limited attention (Naylor 2000). The difficulty quantifying the economic value of goods and services provided by ecosystems, i.e., ecological economics (see Saghoff 1995, Daly 1995), further constrains assessment of economic impacts of invasive plants. Attempts have been made to assess the impact of invasive plants on rangeland economic value and enterprise net returns. Bioeconomic models were developed to estimate direct and indirect economic impacts of leafy spurge (Leitch et al. 1996) and spotted knapweed (Hirsh and Leitch 1996). The economic impact of leafy spurge in Montana, North Dakota, South Dakota, and Wyoming is estimated at $130 million each year (Leitch et al. 1996). Spotted knapweed costs Montana ranchers an estimated $11 million annually (Hirsh and Leitch 1996) and if allowed to spread, cost to Montana's livestock industry could exceed $155 million each year.

Invasion Process

Invasive plants can alter ecosystem processes and plant community successional trajectories. When describing the invasion process, it is important to consider invasion as a component of succession. Johnstone (1986) defines succession as the change in species composition over time. The rate and direction of succession depends on the interaction of species invasion and the reaction of the species in the plant community. Succession is influenced by 3 general factors: site availability; species availability; and species performance (Table 1) (Pickett et al. 1987). These factors are affected by various processes including disturbance and plant:plant and plant:animal interactions that can be modified to alter succession. Succession can be predicted and manipulated with sufficient information about disturbance regime, site, species, and management tools.

Table 1. General causes of ecological succession, contributing processes, and modifying factors (Pickett et al. 1987).

General causes	Contributing Process	Modifying factors
Site availability	Disturbance	Size, severity, time, dispersion
Species availability	Dispersal	Landscape configuration, dispersal agents
	Propagules	Land use, time since last disturbance
	Resources	Soil, topography, site history
Species performance	Ecophysiology	Germination response, assimilation rates, growth rates, genetic differentiation
	Life history	Allocation, reproductive timing, mode of reproduction
	Stress	Climate, site history, prior occupants
	Competition	Competition, herbivory, resource availability
	Allelopathy	Soil chemistry, microbes, neighboring species
	Herbivory	Climate, predators, plant defenses, patchiness

A conceptual framework to describe plant invasion can be useful in understanding the invasion process and in making management decisions. Williamson (1996) provided a structure to organize invasion process information. He partitioned the process into 4 phases: (1) arrival and establishment; (2) spread; (3) equilibrium and effects; and (4) implications. Within each of these phases there are specific conceptual points, which further describe the invasion process. The first 3 phases represent the beginning, middle, and end of the process. The fourth phase describes the consequences of invasion on the community or ecosystem.

The invasion process begins with the arrival of alien plant propagules at the new site. Within the last 500 years, movement of alien plants has been accelerated by human-related activities, through intended or non-intended introductions (Crosby 1986, Di Castri 1989). Geographic distances and physical barriers, mountain ranges and oceans, are reduced as impediments to movement of alien species given the increased efficiency and speed with which man transports materials around the world. Mack (1989) indicated that temperate grasslands outside Eurasia have been forever changed by human activities that have facilitated the introduction of alien plants. He wrote, "Few other changes in the distribution of the earth's biota since the end of the Pleistocene have been as radical." Many of the plants that have invaded the New World originated in the Mediterranean Basin and steppes of the Middle East (Heywood 1989). These regions have been subjected to a long history of human habitation and many plants arising from these regions co-evolved with agricultural practices. This association with agricultural production systems has enhanced development of invasive traits in plants. Introductions of alien organisms continue today despite global implementation of quarantine programs for agricultural pests (Mooney and Drake 1989).

Once the alien plant arrives at a new site, community invasion is regulated by characteristics of the invading plant and the existing community (Lawton 1986). Various, often interrelated, hypotheses about species and site invasive characteristics have been generated to provide a framework for ecological theory of invasion (Cronk and Fuller 1995). The ***absence of predator hypothesis*** proposes that invasive plants have an advantage because they are introduced into new environments without natural enemies from their native range. The ***greater reproductive potential hypothesis*** indicates that invasive plants are more fecund than native species. The ***poorly adapted native species hypothesis*** proposes that invasive plants exhibit a greater tolerance to resource constraints than do native species. The ***chemical change hypothesis*** suggests that invasive plants are better adapted to altered chemical status of an invaded site. The ***balance of nature hypothesis*** is centered on the concept that species-rich communities are more resistant to invasion than species-poor communities. The ***empty-niche hypothesis*** contends that invaded communities contain unoccupied niches ready for habitation by invasive plants. The ***disturbance-produced***

gaps hypothesis suggests that some level of disturbance is necessary to allow an invading species to gain a foothold in a community. These hypotheses provide a foundation upon which to build theory and, ultimately, to predict species invasions.

Attempts to classify species according to their invasiveness have resulted in listings of genetic, physiological, and ecological attributes most often associated with successful invaders (Baker 1965, 1986, Baker and Stebbins 1965, Gray 1986, Lonsdale 1994). Mack (1996) reviewed the advantages and disadvantages of approaches to assess plants invasiveness. These approaches included: listing traits of the invasive plant; characterizing the native range of the invasive plant; developing models to predict invasiveness; quantifying growth characteristics of the invasive plant under different conditions in controlled environments; comparing characteristics of invasive and non-invasive cogeners; and planting the species in the field with and without manipulation of resources. Panetta (1993) and Reichard and Hamilton (1997) suggest that the best predictor of whether or not a species would become invasive in a new environment was its invasiveness elsewhere. Nobel (1989) determined that high population numbers at any life stage in the native environment was a good indicator of invasiveness, while adult and seed longevity and plant perenniality were not reliable indicators of invasive potential. He concluded that knowledge of the invaded environment was as important as the characteristics of the invading species in predicting the invasion process.

To continue the invasion process, alien plant propagules must be dispersed into the new site and arrive at microsites that provide an environment conducive to plant establishment. The location where the immigrant plant can germinate and grow has been referred to as a "safe site" (Harper 1977), "regeneration niche" (Grubb 1977), or "invasion window" (Johnstone 1986). Safe sites meet the requirements of the alien species for germination, growth, and development and enable the plant to reach reproductive maturity.

Disturbance often increases safe site availability for invasive plant establishment (Grubb 1977, Harper 1977, Silvertown 1981, Fox 1985, Hobbs 1991). Various definitions of disturbance have been proposed (Rykiel 1985, Pickett et al. 1987, van Andel and van den Berg 1987, Petraitis et al. 1989, Hobbs and Huenneke 1992). White and Pickett (1985) defined disturbance as any relatively discrete event in time that disrupts ecosystem, community, or population structure, and changes resources, substrate availability, or the physical environment. Events that affect resource availability and community demographic processes such as fire, storms, floods, grazing management, and fertilization are considered to be disturbances. Roads are disturbances that provide corridors for invasive plant dispersal (Lonsdale and Lane 1994, Parendes and Jones 2000) and alter the physical and chemical components of the environment (Trombulak and Frissell 2000), which further facilitate invasion. Disturbances associated with global change (global warming, increasing atmospheric CO_2, increasing nitrogen deposition, etc.) will likely influence distributions of invasive plants (Bazzaz 1990, Johnson et al. 1993, Patterson 1995, Vitousek et al. 1997, D'Antonio 2000, Dukes 2000).

Disturbance is an important factor affecting community structure and dynamics (Cooper 1926, Watt 1947, Elton 1958) that promotes invasion by alien plant species (Ewel 1986, Fox and Fox 1986, Hobbs 1989, 1991, Forcella and Harvey 1983, Pickard 1984), especially where disturbance disrupts species interactions and reduces competition (Crawley 1986, 1987, Kruger et al. 1986, Macdonald et al. 1986, Crawley 1987, Orians 1986, Fox and Fox 1986). Invasion success appears to be dependent on the extent and type of disturbance, propagule pressure (number of alien plant propagules in the community and duration of community exposure to propagules) (Rejmanek 1989), and time interval between disturbance events (Hobbs and Huenneke 1992). Community susceptibility to invasion is increased when disturbances deviate from historical patterns because the resident species are not adapted to the new disturbance regime (Burke and Grime 1996). Managing invasive plants requires manipulating the process of disturbance to favor desirable species.

Species diversity may be another factor that influences community invasibility. A commonly cited concept is that community invasibility increases as the number of species decreases (Elton 1958, Rejmanek 1989, Lodge 1993, Tilman 1996, 1997, 1999). Proposed mechanisms that support this premise are that diverse communities have a greater variety of ways to capture resources or possess species that more fully utilize resources than less diverse communities (Naeem et al. 1994, Tilman 1997); therefore, niches are already occupied when a potential invader arrives.

There is evidence that species-rich communities contain a greater number of alien species than species-poor communities (Pickard 1984, Knops et al. 1995, Robinson et al. 1995, Planty-Tabacchi et al. 1996, Palmer and Maurer 1997). Following an analysis of data collected from 184 sites, Lonsdale (1999) determined that communities richer in native species contained more alien plants than species-poor communities. There was no causal relationship between native and invasive plant diversities when measured at the community scale. Low-diversity shortgrass steppe and dry meadow communities were more resistant to invasion than high-diversity wet meadow and riparian communities (Stohlgren et al. 1998, 1999). They suggested that shortgrass steppe and dry meadow communities resist invasion because of the low levels and availability of resources (soil nutrients and water), which are essentially monopolized by the native vegetation. In contrast, high diversity communities are relatively resource rich, and resources become available following disturbance that can be exploited by invading species.

Disturbance appears to be critically important in the beginning of the invasion process because it creates openings for alien plants to occupy. Fluctuations in local species abundance in species-rich communities may provide an opening for alien plants to become established (Peart and Foin 1985). Elton (1958) indicated that the lack of invaders into a given community was the result of competitors, predators, parasites, and diseases that enabled the community to resist invasion. Invasions were successful only when these barriers were reduced or removed by disturbance, or in the case of an alien species, natural enemies were left behind in the native habitats. In contrast, Simberloff (1989) suggested that the vulnerability of a community to invasion was not because of these barriers, but rather the greater frequency of human-mediated introductions of alien species into disturbed communities. Obviously, the invasion process can be affected by a multitude of interacting factors including those described by Elton (1958) and Simberloff (1989).

Once alien species establish, the next phase is their spread through the community (Williamson 1989, Elton 1958, Okubo 1980). An important component of spread is the rate at which the invading species colonizes new sites in the community (Mooney and Drake 1989). Rate of spread is a function of both the alien species characteristics and the characteristics of the ecosystem through which the species spreads. Moody and Mack (1988) indicated that the rate of spread of an invader will be geometric if spread is from widely spaced patches versus a linear rate if spread is from a "nascent foci" or single patch. Early in the invasion process there is a lag phase where the invasive plant populations remains small and localized for long periods before expanding exponentially (Fig. 1) (Mack 1985, Auld and Tisdell 1986, Braithwaite et al. 1989, Griffin et al. 1989, Lonsdale 1993, 1999). Hobbs and Humphries (1995) attributed this lag phase to several factors including the time needed for the invading plant to adapt to the site before spreading rapidly, the invading plant's requirement for a specific event or series of disturbance events that facilitate rapid spread, or the invading plant is simply not noticed until it becomes widespread.

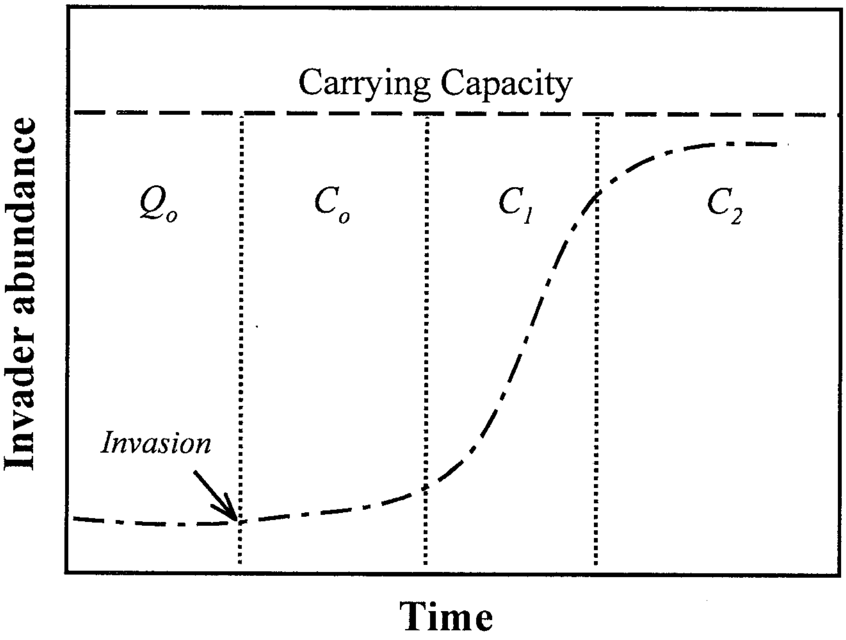

Fig. 1. Phases of weed invasion and priorities for action at each phase: Q_0—quarantine priority phase; C_0—eradication priority stage; C_1—control priority phase (exponential growth phase); C_2—maximum population level, effective control unlikely without massive resource inputs. Ease of treatment declines and difficulty and cost increases moving from left to right (Hobbs and Humphries 1995 after Chippendale 1991).

Integrated Invasive Plant Management

Integrated weed management evolved from the concept of integrated pest management in agricultural crops. Integrated pest management was developed by entomologists during the late 1950s in response to problems created by excessive use of insecticides (Thill et al. 1991), and was supported by public concerns about environmental consequences of pesticide use that were catalyzed by Rachel Carson's ***Silent Spring*** (1962). Integrated pest management has been defined in a number of ways. Two common definitions are that this management strategy involves: (1) a combination of biological, chemical, and cultural methods for maintaining pests below economic crop injury thresholds (Burn et al. 1987, Flint and van den Bosch 1983) or (2) non-chemical pest control measures to reduce reliance on chemical pesticides (Goldstein 1978). Integrated pest management programs should be developed from interdisciplinary efforts that gather information about: (1) the ecological basis of the pest problem; (2) how to make the crop environment unfavorable for pests; (3) when pesticide treatments are needed based on pest and natural enemy populations dynamics; and (4) benefits and risks of the integrated pest management strategy for agriculture and society (Pimental 1982).

Integrated weed management emerged as a viable concept among crop weed scientists in the 1970s. Integrated weed management was defined as the application of technologies in a mutually supportive manner, and selected, integrated, and implemented with consideration of economic, ecological, and sociological consequences (Walker and Buchanan 1982). Shaw (1982) indicated that integrated weed management is an approach in which principles, practices, methods, and strategies are chosen to control pests, while minimizing undesirable results. Thill et al. (1991) defined integrated weed management as the integration of effective, environmentally safe, and sociologically acceptable control tactics that reduce weed interference below the economic injury level. Sheley et al. (1996), emphasizing management and not control of noxious rangeland weeds, indicated that integrated weed management strives to use the most economically, ecologically, and environmentally effective combination of principles, technologies, and systems to meet management goals.

Integrated weed management provides a context for managing pests that is ecosystem-centered, and not specific to a species or pest control technology. Frequently, the stated or implied goal of integrated weed management is pesticide-use reduction. We believe that this is not in keeping with the basic concept of integrated weed management, which is a sustainable approach to managing pests by combining biological, cultural, mechanical and chemical tools that minimize economic, health and environmental risks (U.S. Congress, Office of Technology Assessment 1993). Placing value-laden judgements on the various pest management tools and ranking them according to subjective criteria should be avoided. All available tools should be considered during development of integrated weed management programs and those selected should optimize attainment of specific management objectives.

Developing effective integrated weed management programs requires a thorough understanding of the biology and ecology of the invasive plant and invaded community. Information about plant demography, propagule dynamics, seedling recruitment, plant growth and development, and methods of reproduction could help identify vulnerabilities to be exploited in integrated weed management systems (Radosevich et al. 1997). In addition, it is critical that the causes of plant invasion be understood so that they can be alleviated (Hobbs and Norton 1996).

Adapting the basic concepts of integrated weed management on cropland to integrated weed management on rangeland appears relatively straightforward. However, there are differences in management intensity and management objectives between cropland and rangeland that need to be considered. First, monocultures of agronomic species are grown on cropland and are often intentionally disturbed several times during the production cycle. Cropland is managed intensively and resource inputs, e.g., pesticides, fertilizer, and cultivation, often improve economic returns. In contrast, rangeland supports heterogeneous mixtures of plant species and is managed extensively. The relatively low value of rangeland per unit area reduces the economic viability of resource inputs compared with cropland. Second, identification of economic thresholds of injury caused by pests are central to development of integrated weed management programs in cropland. Determining economic thresholds for rangeland invasive plants is difficult and has not been adequately addressed. Furthermore, control of rangeland invasive plants designated as noxious is often mandated by law without regard to economic thresholds. Finally, impacts of invasive plants on rangeland ecosystem function and structure may be of more concern than economic impacts, especially on rangeland where other products besides livestock, e.g. wildlife, recreation, aesthetics, and water, are important.

Invasive Plant Management Strategy Components

The magnitude and complexity of rangeland weeds, combined with the costs for their control, necessitate the use of integrated weed management (Sheley et al. 1996). Education, prevention, detection, monitoring and assessment, and weed control methods are key components of integrated management strategies. Education is an under-emphasized, but important part of invasive plant management. Public awareness about the ecological, environmental, and economic impacts associated with invasive plants may help provide the political support and resources necessary for invasive plant management. Awareness also can promote activities, such as early detection of newly arriving species, in which the general public can participate. On-going educational programs provide practitioners and the general public with knowledge of current management strategies essential to sustainable invasive plant management.

Preventing invader introduction by restricting movement of propagules from infested areas can minimize invader dispersal into new habitats. Early detection followed by swift, intensive, and aggressive implementation of effective control measures during the invasion lag phase (Fig. 1) are essential to eliminate the invader, or at least to prevent seed production (Zamora et al. 1989). Once the invasion process is in the exponential phase, eradication of the invader is usually not a realistic goal. Instead, the emphasis should be to reduce the impact of the invader to an acceptable level and keep the plant from dominating the plant community and substantively altering ecosystem processes. After the invader has reached its maximum abundance, containment of the invader or implementation of intensive restoration efforts may be the only feasible management options.

Monitoring and assessment of invasive plant distributions during invasion and in conjunction with management provides the basic information necessary for planning (Cooksey and Sheley 1997, Johnson 1999). Remote sensing tools such as aerial videography, geographic information systems, global positioning systems, and satellite-borne, narrow-band, multispectral imaging technology have the potential to improve accuracy and reduce the time needed to assess invasive plant distributions (Everitt et al. 1995, 1996a, 1996b, Bork et al. 1998). Time-repeated surveys allow continual assessment of management effectiveness and provide the information necessary to modify strategies to optimize management. Knowledge of invasive and native plant distributions is important for developing invasion risk assessment models based on invasion dynamics, environmental characteristics, and weed dispersal processes.

An adaptive management approach can complement integrated programs to manage invasive plants on rangeland. This approach requires establishing management goals, developing and implementing management programs based on the goals, monitoring and assessing impacts of management efforts, and modifying goals and invasive plant management in light of new information (Schwarz and Randall 1995, Randall 1997). Adaptive management has been developed as an integrated, multidisciplinary approach to deal with the uncertainty associated with natural resource management (Holling 1978, Walters 1986, Gunderson 1999). This approach provides a way to move from a reactive to a proactive mode of invasive plant management.

Weed Control Methods

Biological. Quimby et al. (1991) defined biological control of weeds as the planned use of living organisms to reduce the plant's reproductive capacity, density, and effect. Biological control can involve any of 3 strategies: conservation; augmentation; and importation of natural enemies (Harley and Forno 1992). Conservation involves manipulation of the environment to enhance the effect of existing natural enemies and is usually used to manage native weeds. Augmentation employs periodic release of natural enemies and is restricted to managing weeds in high-value food crops because it requires large investments of time and money and repeated intervention. Importation, also known as ***classical biological control***, is the planned relocation of natural enemies of exotic weeds from their native habitats onto weeds in their naturalized habitats. This strategy seeks to reestablish weed and natural enemy interactions that reduce the weed population to an acceptable level (DeBach and Rosen 1990). Synchrony in the life cycles of host plant and agent, adaptation of the agent to a new climate and habitats, ability of the agent to find the host at varying densities, capacity of the agent to reproduce rapidly, and the nature, extent, and timing of the damage caused by the biocontrol agent are among the factors that determine biocontrol agent effectiveness (Louda and Masters 1993).

Success of biological weed control during the past 200 years has been variable. Julien (1992) documented 610 biological control projects that involved 94 weed species in 53 countries. There have been some phenomenally successful biocontrol projects including control of *Opuntia* spp. in Australia by the moth *Cactoblastus cactorum* and control of St. Johnswort (*Hypericum perforatum* L.) in the Pacific Northwest by the beetles, *Chrysolina quadrigemina* and *C. hyperici*. There are 72 examples worldwide where weed biocontrol programs have been underway for a sufficient period to assess control. Of these programs, 28% have resulted in control that could be rated as sometimes complete (Sheppard 1992). In contrast, no control was achieved in 35% of these programs even though biological control agents were established. Important factors that have contributed to the limited success of biological weed control programs include a high level of genetic diversity in the target species, limited compatibility of agents with the invasive plant genotype, and opportunistic predation and parasitism of biocontrol agents in the introduced environment (Sheppard 1992).

The release of imported biological control agents on invasive plants is not without risk (Harris 1988, Howarth 1991, Follett and Duan 1999). By its very nature, classical biocontrol involves release of alien organisms to control other alien organisms and alter botanical composition. The consequences of natural enemy utilization of native relatives of the alien weeds are considered a potentially detrimental side effect of biocontrol (Harris 1988, 1990, Ehler 1990, Howarth 1991). Within a decade after release of 2 beetles, *Chrysolina quadrigemina* and *C. hyperici*, to control St. Johnswort (Huffaker and Kennett 1959), larvae of *C. quadrigemina* were found feeding on an introduced ornamental, *H. calycinum* L., and to a limited extent on a related native species, *H. concinnum* Beth (Andres 1985). The seedhead weevil, *Rhinocyllus conicus* Froel., introduced from Europe into North America to control musk thistle (*Carduus nutans* L.) (Kok and Surles 1975) has been reared from flowerheads of several native *Cirsium* species in California (Goeden and Ricker 1986, 1987, Turner et al. 1987). It has also reduced seed production of native *Cirsium* species at several locations in the central Great Plains (Louda et al. 1997). Once an insect is released into a new environment, little can be done to restrict its distribution or host affinity. Monitoring candidate biological control agents for range expansions, host shifts, and effects on related nontarget plants is critical (Howarth 1991).

Genetic variation in populations of the natural enemy and invasive plant can influence biocontrol program success (Roush 1990). High levels of genetic variability in traits that influence insect impact should increase the probability that the insect will adapt to the new environment. Furthermore, genetic variation extends the range over which the natural enemy can occur and utilize the weed (Harris and Peschken 1971). Identification of important genetic variation and its maintenance in importation, mass-rearing, and release should enhance chances of success. Biological diversity is usually highest in the center of origin of a taxon (Vavilov 1992) and the greatest genetic variation in the natural enemies may be found in the areas of weed origin (Bartlett and Van den Bosch 1964, Zwolfer et al. 1976).

Molecular biology offers tools to quantify invasive plant genetic diversity and to better match natural enemies with the target invasive plant (Nissen et al. 1995, Rowe et al. 1997). Taxonomists, evolutionary biologists and breeders use molecular techniques to measure plant genetic diversity and determine how plants are related. Selected DNA-based molecular marker techniques offer an approach to quantify invasive plant genetic diversity in native and introduced habitats and provide a better understanding of the complex relationships between invasive plants and potential biocontrol agents. This information could provide insights into the geographic origins of invasive plants and provide a means to direct the search for compatible biocontrol agents.

Chemical. Herbicides are assigned to groups according to their chemistry and mode of action (Devine et al. 1993, Ross and Lembi 1999) (Table 2). Mode of action refers to the system, process, or tissue affected by the herbicides. A herbicide is usually selective within certain rates, environmental conditions, and methods of application. Foliar-active herbicides are applied directly to the leaves or stems of plants where they are absorbed and translocated in the plant. These herbicides may or may not remain active once moved into the soil. Soil-active herbicides are absorbed by the roots from the soil water solution. Herbicides can be categorized as to whether they are applied before planting and before (preemergence) or after (postemergence) weed emergence.

Herbicides have been the dominant tools used to control invasive plants on rangeland (Bovey 1995). Potential for ground or surface water contamination, adverse effect on desirable plants, and cost of repeated application to control weeds are some of the concerns associated with herbicide use. The myriad of herbicides currently available, with different modes of action and selectivity, provide land managers with many options to control undesirable plants and manipulate plant composition (Table 2). The most commonly used herbicides on rangeland are auxin-like growth regulators (phenoxy, benzoic, or picolinic acid herbicides) that selectively control broadleaf plants and do not injure grasses when used at recommended rates.

Glyphosate[1] used on rangeland to control grass and broadleaf weeds, which has no activity in the soil. This is a postemergence herbicide that is translocated within the plant and selectivity is usually determined by the plant growth status. Control is optimized if the target plant is growing at the time of application and negated when the plant is dormant. In the Great Plains, glyphosate was applied in the fall to control cool-season grasses, such as Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* L.), but will not injure warm-season grasses that are dormant at application time (Bush et al. 1989).

The imidazolinone and sulfonylurea herbicides: disrupt the synthesis of amino acids, leucine, isoleucine, and valine, that are essential for plant growth and development; are phytotoxic at very low rates; and have low toxicity to vertebrates and invertebrates. Imazapic applied at 140 to 210 g ai ha^{-1}, controls leafy spurge (Masters et al. 1998, Thompson et al. 1998) and is tolerated by many species in the Gramineae, Fabaceae and Compositae families. Another unique attribute of imazapic and other imidazolinone herbicides is the ability to control many annual grass and broadleaf weed species during establishment of desirable native warm-season grasses, forbs, and legumes (Masters et al. 1996, Frye et al. 1997, Rivas-Pantoja et al. 1997, Beran et al. 1999a, 1999b, 2000). Imazapyr controls saltcedar in New Mexico when applied at 0.56 to 0.84 kg ai ha^{-1} in late summer to early fall (Duncan and McDaniel 1998). Sulfometuron is currently registered to control cheatgrass, medusahead [*Taeniatherum caput-medusae* (L.) Nevski], and cheat (*Bromus secalinus* L.) on non-cropland administered by state and federal land management agencies in the Intermountain West (EPA Registration No. 352-401).

Cultural. Cultural practices include fire, grazing, revegetation or reseeding, plant competition, and fertilization. These methods are generally aimed at enhancing desirable vegetation to minimize weed invasion.

Fire, along with climate and herbivory, were the primary forces responsible for the formation and maintenance of grassland ecosystems in North America (Wright and Bailey 1982). As with any disturbance, fire effects on ecosystems are influenced by its frequency, intensity, season of occurrence, and interactions with other disturbances. North American grassland fire regimes were shaped by sources of ignition, lightning and humans, and climate (Pyne 1984). Fire is a useful, if not essential, practice to meet management objectives for many plant communities in North America (Wright and Bailey 1982).

Selectivity by herbivores alters competitive interactions within plant communities (Crawley 1983, Luken 1990). In some situations sheep or goat grazing (Bowes and Thomas 1978, Landgraf et al. 1984, Walker et al. 1994, Lym et al. 1997) can control leafy spurge. Appropriate grazing by animals preferring weeds can shift the plant community toward more desired species (Walker 1994, 1995). In contrast, excessive cattle grazing without periodic rest can selectively reduce grass competitiveness, shifting the competitive advantage to weeds (Svejcar and Tausch 1991).

Revegetation with desirable plants may be the best long-term alternative for managing weeds on sites that lack suffi-

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[1] Refer to Table 2 for chemical names of herbicides mentioned in text.

Table 2. Selected herbicides that are currently registered for use on rangeland, pastures, or non-cropland.[1]

Chemical group	Common name	Chemical name	Mode of action	Plants controlled[2]	Activity[3]	Application timing[4]
Benzoic acid	Dicamba	3,6-dichloro-2-methoxybenzoic acid	Auxin-type growth regulator	B	F, S	PRE, POST
Benzonitrile	Bromoxynil	3,5-dibromo-4-hydroxybenzonitrile	Photosynthetic inhibitor	B	F	POST
Bipyridilium	Paraquat	1,1'-dimethyl-4,4'-bipyridinium ion	Photosystem 1 energized cell membrane disrupter	B, G	F	POST
Semicarbazones	Diflufenzopyr	2-[1-[[[(3,5-difluorophenyl)amino] carbonyl]hy-drazono]ethyl]-3-pyridine-carboxylic acid	Auxin transport inhibitor	B	F	POST
Imidazolinone	Imazethapyr	2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid	Branched-chain amino acid inhibitor	B, G	F, S	PRE, POST
	Imazapyr	2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid	Branched-chain aminor acid inhibitor	B, G	F, S	PRE, POST
	Imazapic	2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-methyl-3-pyridinecarboxylic acid	Branched-chain amino acid inhibitor	B, G	F, S	PRE, POST
Phenoxy acid	2,4-D	(2,4-dichlorophenoxy)acetic acid	Auxin-type growth regulator	B	F	POST
	2,4-DB	4-(2,4-dichlorophenoxy)butanoic acid	Auxin-type growth regulator	B	F	POST
	MCPA	(4-chloro-2-methylphenoxy)acetic acid	Auxin-type growth regulator	B	F	POST
Phenylurea	Diuron	N'-(3,4-dichlorophenyl)-N,N-dimethylurea	Photosynthetic inhibitor	B, G	F, S	PRE, POST
	Tebuthiuron	N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea	Photosynthetic inhibitor	B, G	F, S	PRE, POST
Picolinic acid	Clopyralid	3,6-dichloro-2-pyridinecarboxylic acid	Auxin-type growth regulator	B	F, S	PRE, POST
	Picloram	4-amino-3,5,6-trichloro-2-pyridine-carboxylic acid	Auxin-type growth regulator	B	F, S	PRE, POST
	Triclopyr	[(3,5,6-trichloro-2-pyridinyl)oxy]acetic acid	Auxin-type growth regulator	B	F, S	PRE, POST
s-Triazine	Atrazine	6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine	Photosynthetic inhibitor	B, G	F, S	PRE, POST
	Hexazinone	3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione	Photosynthetic inhibitor	B, G	F, S	PRE, POST
	Simazine	6-chloro-N,N'-diethyl-1,3,5-triazine-2,4-diamine	Photosynthetic inhibitor	B, G	F, S	PRE, POST
Sulfonyl urea	Chlorsulfuron	2-chloro-N-[[(4-methoxy-6-methyl-1,3,5-triazin- 2-yl)amino]carbonyl] benzenesulfonamide	Branched-chain amino acid inhibitor	B, G	F, S	PRE, POST
	Metsulfuron	2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl) amino] carbonyl]amino] sulfonyl] benzoic acid	Branched-chain amino acid inhibitor	B, G	F, S	PRE, POST
	Sulfometuron	2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino] car-bonyl] amino]sulfonyl]benzoic acid	Branched-chain amino acid inhibitor	B, G	F, S	PRE, POST
Uracil	Bromacil	5-bromo-6-methyl-3-(1-methylpropyl)-2,4(1H, 3H)pyrimidinedione	Photosynthetic inhibitor	B, G	F, S	PRE, POST
Unassigned	Fosamine	ethyl hydrogen (aminocarbonyl)phosphonate	Unknown	B	F	POST
	Glyphosate	N-(phosphonomethyl)glycine	Aromatic amino acid inhibitor	B, G	F, S	POST
	Quinclorac	3,7-dichloro-8-quinolinecarboxylic acid	Cell wall formation inhibitor	B, G	F, S	PRE, POST

[1] Chemical group and mode of action from Ross and Lembi (1999) and common name and chemical names from (Weed Science Society of America 1994).

[2] B = broadleaf species and G = grass species

[3] F = taken up by plant foliage and S = has activity in the soil

[4] PRE = applied before plant emerges and POST = applied after plant emerges

cient abundance of desirable species. Establishing competitive grasses, forbs, and legumes may suppress invasive plants, enhance plant community resistance to further invasion, and improve forage production and quality (Masters et al. 1996, Lym and Tober 1997, Bottoms and Whitson 1998, Ferrell et al. 1998, Masters and Nissen 1998, Whitson and Koch 1998).

Selecting plant species is a critical consideration when developing a desired plant community if the desirable species are not present in sufficient abundance to enable regeneration within an acceptable timeframe. Jones and Johnson (1998) described an integrated approach for making decisions about how to select plant materials for rangeland revegetation. Site potential, desired landscape, seeding objectives, conflicting land-use philosophies, appropriate plant materials, invasive plants, community seral status, and economic limitations are key components of the decision-making process.

Table 3. Examples of integrated strategies for control of invasive plants on rangeland (modified after DiTomaso 2000).

Invasive Plant	Strategy components	Citation
Acroptilon repens (L.) DC	Tillage, herbicide, and revegetation	Dershied et al. 1963, Bottoms and Whitson 1998, Benz et al. 1999
Bromus tectorum L.	Tillage, herbicide, and revegetation	Eckert and Evans 1967, Evans et al. 1967 Whitson and Koch 1998
	Herbicide and grazing	Whitson and Koch 1998
Centaurea spp.	Herbicide, revegetation, and biocontrol	Enloe and DiTomaso 1999
	Herbicide and revegetation	Sheley et al. 2001
	Burning and herbicide	Lacey et al. 1995
Cirsium arvense (L.) Scop.	Herbicide and revegetation	Wilson and Kachman 1999
Euphorbia esula L.	Herbicide and biocontrol	Nelson et al. 1998
	Tillage, herbicide, and revegetation	Selleck et al. 1962, Ferrell et al. 1998 Lym and Tober 1997
	Tillage, herbicide, and fertilization	Lym and Messersmith 1993
	Grazing and herbicide	Lym et al. 1997
	Herbicide, burning, and revegetation	Masters and Nissen 1998, Masters et al. 2001
Hypericum perforatum L.	Tillage and revegetation	Gates and Robocker 1960
Lepidium latifolium L.	Mowing and herbicide	Renz and DiTomasa 1999
Linaria dalmatica (L.) Mill.	Tillage and revegetation	Gates and Robocker 1960
Opuntia stricta (Haworth) Haworth	Herbicide and biocontrol	Hoffman et al. 1998
Taeniatherum caput-medusae (L.) Nevski	Burning, herbicide, and revegetation	Horton 1991
	Tillage, herbicide, and revegetation	Young et al. 1969

A question faced by land managers considering revegetation is whether to use native and/or introduced plant materials (Lesica and Allendorf 1999). The value of local ecotypes (Knapp and Rice 1994, Linhart and Grant 1996), native or introduced plant cultivars with improved agronomic traits developed by formal breeding programs (Vogel et al. 1989, Vogel 2000, Casler et al. 1996), and mixed populations or hybrid genotypes (Millar and Libby 1989, Munda and Smith 1995) in revegetation programs has been detailed. Another perspective is that rather than emphasizing individual species, the focus of revegetation programs should be on establishing functional groups (Walker 1992) that maintain ecosystem processes (Noss 1991). Johnson and Mayeux (1992) argue that no special quality should be attributed to a species labeled as a "native," rather the focus should be on ecosystems as "self-sustaining systems in terms of physiognomic structure and functional processes in which various species . . . . . are interchangeable."

Mechanical. Mechanical treatments involve either removal of the aerial portions of the weed or removal of enough of the root and crown to kill the plant. Annuals and some biennials and perennials can be suppressed or controlled if mowing occurs before fruits mature and viable seeds form. Mowing in the fall for 3 consecutive years decreased spotted knapweed density about 85% compared to areas that were not mowed (Rinella et al. 2001). Mowing perennial herbaceous or woody plants that have the capability to reproduce vegetatively can actually exacerbate weed interference by stimulating production of new stems from vegetative buds below the cut surface. However, perennial plants that reproduce vegetatively can be severely damaged or killed by tillage (Derscheid et al. 1985), bulldozing, root-plowing, or grubbing (Vallentine 1989). The high cost of these mechanical treatments limits their use to control rangeland weeds.

Integrating Multiple Weed Control Strategies

There are several examples of integrated strategies used to manage invasive plants and improve rangeland communities (Table 3). Efforts to assess the compatibility of insect biocontrol agents and herbicides during development of integrated management systems are increasing (Messersmith and Adkins 1995). Revegetation has been a common component of integrated approaches because it is essential that desirable plant species, rather than another invasive plant species, fill the niche vacated by the controlled invader. Herbicides and tillage were used to suppress dalmation toadflax (*Linaria dalmatica* Mill.) and St. Johnswort (Gates and Robocker 1960), cheatgrass (Eckert and Evans et al. 1967), and medusahead (Young et al. 1969) in early attempts to prepare degraded rangeland sites for revegetation with cool-season grasses.

Approaches that include herbicide application and establishing monoculture stands of introduced and native perennial grasses have been successfully used to suppress leafy spurge and improve forage production on rangeland. In Wyoming, seedbed preparation consisted of multiple glyphosate applications in spring and summer followed by tillage before planting introduced cool-season grasses (Ferrell et al. 1998). Introduced cool-season grasses were planted in a tilled seedbed following broadcast applications of glyphosate and 2,4-D in North Dakota (Lym and Tober 1997). The planted grasses that were most effective in suppressing leafy spurge were 'Bozoisky' Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] and 'Luna' pubescent wheatgrass [*Elytrigia intermedia* (Host) Beauv.] in Wyoming, and 'Rebound' smooth brome and 'Reliant' intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkw. & D.R. Dewey] in North Dakota. In Nebraska, monoculture stands of native warm-season grasses, big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.), were established on leafy spurge-infested rangeland and increased herbage yields by more than 40% and reduced leafy spurge density and yield (Masters and Nissen 1998). The sites were treated with imazapyr and sulfometuron in the fall and burned the following spring before tallgrasses were planted into the herbicide-suppressed sod without tillage.

Recent rangeland improvement research demonstrated an integrated weed management strategy, which suppressed leafy spurge and associated vegetation and facilitated planting and establishment of stands of mixture of native warm-season grass and legume species (Masters et al. 2001). These multi-species assemblages may more fully use resources on degraded rangeland and preempt resource use by less desirable species, including leafy spurge. The strategy consisted of herbicide application, burning the herbaceous standing crop, and planting mixtures of native species without tillage. Glyphosate and imazapic were the herbicides selected to suppress existing resident vegetation, while not interfering with establishment of species in the planted mixtures. Glyphosate controlled cool-season grasses that were growing at the time of application, but provided no residual weed control. Imazapic provided residual control of leafy spurge and annual grass and broadleaf plants and was tolerated by a number of warm-season grasses (Rivas-Pantoja et al. 1997, Beran et al. 2000), forbs (Beran et al. 1999a) and legumes (Beran et al. 1999b).

Invasive Plant Management Systems as a Component of Rangeland Resource Management

To be successful, invasive plant management programs must be compatible with and integrated into overall rangeland resource management objectives and plans. Effective invasive plant management programs cannot be developed without considering other management components that impinge upon the rangeland resource. Integrating all components within the rangeland resource management program is essential because interactions among the components determine the economic and ecological sustainability of the program. For example, altering grazing management or fire regimes impact site invasibility since the invasion process can be influenced by disturbance.

What is the appropriate goal when developing rangeland resource management programs? The “desired plant community” could serve as the goal for rangeland resource management. The desired plant community concept originated with the USDI-Bureau of Land Management and was defined by the Society for Range Management, Task Group on Unity in Concepts and Terminology (1995) as, “of the several plant communities that may occupy a site, the one that has been identified through a management plan to best meet the plan’s objectives for the site. It (the desired plant community) must protect the site at a minimum.” This concept recognizes that plant community succession for a given site can progress along multiple trajectories and result in different outcomes. Factors that influence these outcomes include past management, plant and animal dispersal from adjacent areas, climatic conditions, disturbance regimes (past, present, and future), and species selected for revegetation projects. The desired plant community concept is consistent with prevailing state and transition (Westoby et al. 1989) and threshold (Laycock 1991, Friedel 1991) models of vegetation change. These non-equilibrium models of succession have superceded the unidirectional Clementsian climax community model (Clements 1916, Weaver and Clements 1938).

The desired plant community is an appealing concept for rangeland management because it empowers land managers to design a plant community that meets management objectives. In the context of invasive plant management, resistance to alien plant invasion would be a key criterion considered when designing a desired plant community. Obtaining the desired plant community involves managing succession, which requires knowledge of the 3 general causes of succession: site availability; differential species availability; and species performance (Table 1) (Pickett et al. 1987, Luken 1990). Within the limits of knowledge about the conditions, mechanisms, and processes controlling plant community dynamics, these 3 components can be modified to manage succession by using designed disturbance, controlled colonization, and controlled species performance (Pickett et al. 1987). Designed disturbances include activities that create or eliminate site availability and control succession such as tillage or herbicide suppression of sod. In successional management, designed disturbances are used to alter successional trajectories and to minimize continual reliance on external inputs. Controlled colonization is the intentional alteration of availability and establishment of plant species by influencing seed banks, vegetative propagule pools, and regulation of safe sites for germination and establishment of desirable species. Invasive plant seed banks can be depleted through attrition if seed production is prevented or reduced. Controlled species performance involves manipulating growth and reproduction of plant species to redirect succession. Biological and chemical weed control, grazing, mowing, fertilization, and planting competitive species can create differential species performance. Management of succession is an ongoing process moving along a trajectory that is driven by both naturally occurring and human-induced processes. A generalized model describes the process of managing succession by using various management tools in appropriate sequences and combinations to achieve a desired grassland community structure (Fig. 2) (Masters and Nissen 1998).

The restoration ecology discipline provides goals to consider when developing and implementing strategies to manipulate community succession to meet management objectives. Restoration has been distinguished from or referred to interchangeably with rehabilitation, reclamation, reconstruction, renovation, and other terms (Whisenant 1999). The Society for Ecological Restoration (1994) defined restoration as the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems, and Jackson et al. (1995) provide further elaboration of the definition. Hobbs and Norton (1996) suggest a broader definition, with restoration occurring along a continuum from rebuilding totally devastated sites to maintaining pristine sites with limited management. They indicate that restoration should be applied at the landscape scale and the goal should be to return degraded ecosystems to conditions that meet conservation and production objectives in a sustainable manner.

Decision Support Systems

Invasive plant management is complex, thus all applicable information should be synthesized and presented in a way that is useful to managers. Decision support systems offer an approach to improve decision making when complex interactions are involved (Stuth and Smith 1993). Expert systems, a form of decision support systems, can improve decision making by using knowledge and experience of experts to provide users a means to assess alternative management outcomes based on specific information about the situation (Barrett and Jones 1989). Many decision support systems use heuristic (“rule of thumb”) approaches to problem-solving that blend hard data with semi-structured procedures and expertise to provide information required to define a problem and possible solutions (Scifres 1987, Stuth and Smith 1993). The integrated brush management system concept developed by Scifres et al. (1983) provides a system to evaluate integrated management with multiple objectives and components. These models could be of great benefit in developing decision support systems for invasive plant management programs.

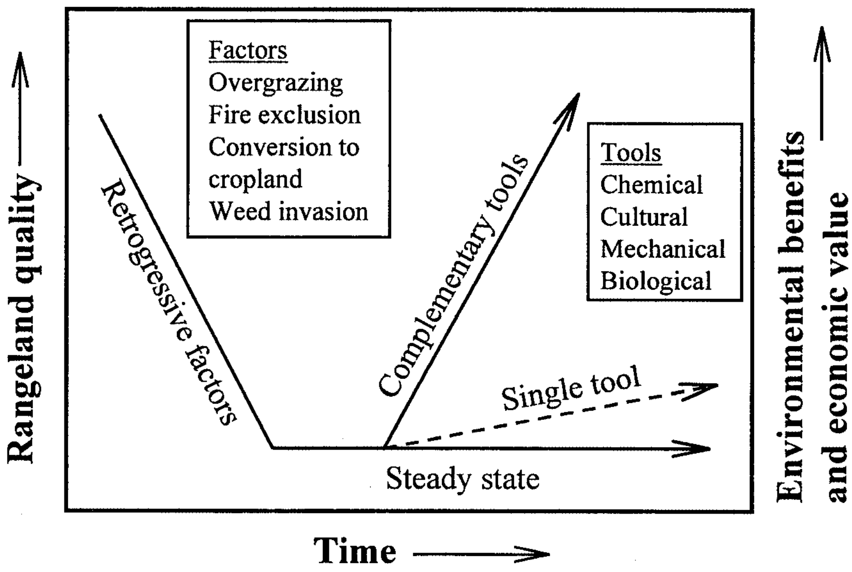

Fig. 2. Generalized community succession model for Great Plains grasslands. Retrogression leads to a steady state condition of low productivity. Reliance on a single technology results in slow grassland recovery rate. Sequential application of complementary and possibly synergistic technologies accelerates progress towards higher quality rangeland (Masters and Nissen 1998).

Conclusion

Invasive plants can have adverse effects on rangeland and pasture ecosystems by disrupting ecosystem processes and reducing their capacity to recover after disturbance. Disturbance is an important factor affecting community structure and dynamics, and facilitates alien plant invasion. Managing invasive plants requires manipulating disturbance regimes to favor desirable species. Various technologies are available for managing invasive plants, but acceptable long-term control will only be achieved when integrated weed management programs are integrated into rangeland resource management plans. Integrated weed management provides a context for managing pests that focuses on ecosystem processes and not on particular plant species or control practices. The advantages and disadvantages of weed control tools will vary according to the invasive plant and invaded site characteristics. The merits of each control measure and the potential for complementary or synergistic interactions when applying measures in appropriate sequences and combinations should be considered when developing integrated weed management programs. The reasons for the arrival, establishment, and spread of invasive plants must be understood before sustained progress can be made toward controlling the plant and improving rangeland and pasture ecosystems. Simply removing invasive plant species with selected control measures may only open niches for other undesirable species to occupy if aggressive desirable species are not available. An appropriate goal of invasive plant management should be to restore desirable native or introduced species communities that are resistant to future invasions. Prevention, detection, and control are key components of integrated management strategies. Early detection followed by prompt implementation of effective control measures is essential to eliminate the invader. Without a commitment to taking swift action, the invasion process will progress into the exponential population expansion phase and eradication of the invader will not be a realistic goal. Invader containment or plant community restoration are the primary options once invader abundance reaches the carrying capacity of the invaded habitat. The desired plant community concept provides a useful goal for invasive plant and rangeland resource management. Ecosystem processes and successional trajectories can be manipulated to achieve the desired plant community by designing disturbance regimes and manipulating dispersal, establishment, and maintenance of desirable species. Development of decision support systems to assist managers in confronting the inherent complexity associated with managing invasive plants and rangeland ecosystems is a critical need.

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Community characteristics of old-growth western juniper woodlands

WENDY SIMS WAICHLER, RICHARD F. MILLER, AND PAUL S. DOESCHER

Authors are graduate student, professor of Rangeland Resources at the Eastern Oregon Agricultural Research Center, and professor of Rangeland Resources, Oregon State University.

Abstract

While considerable attention has been given to the areal expansion of juniper (*Juniperus* sp.) in the western United States, the presence and ecological significance of old-growth juniper communities has gone largely unnoted. Increased recognition of these communities has prompted questions about how to recognize old-growth, community structure, ecological importance, and appropriate management. As an initial analysis of old-growth western juniper woodlands (*Juniperus occidentalis* Hook var. *occidentalis* Vasek) in central Oregon, this study investigated old-growth community structure on eolian-sand derived soils. These woodlands represent the most extensive old-growth western juniper woodlands throughout its range. Nine study plots were established at 7 sites. Within each plot, densities and physical attributes of all live trees and large standing and fallen woody detritus were recorded. Additional measurements for live trees included canopy cover, apparent age class (pre- or postsettlement), and a sampling of tree ages. Aging of trees older than 250 years was complicated by extensive heartwood rot. Shrub density and cover were measured by species. Understory cover was measured by species and functional type. Bare ground, rock, juniper litter, other litter, moss, and cryptogamic crust cover were also measured. Plant cover ranged from 11 to 33% for trees, 0 to 10% for shrubs, 3 to 12% for perennial grasses, 1 to 2% for forbs, and from 0 to 0.1% for annual grasses. The woodlands contained at least 80 trees ha^{-1} aged over 200 years. Correlations between tree parameters and understory structure and composition were generally poor. Differences in plant composition among these stands was primarily attributed to elevation, slope, and percent sand content. Structural characteristics that distinguished old-growth stands from younger stands included tree growth form, presence of standing and dead large woody debris, lichen on dead branches, and a relatively open canopy. Results provide a preliminary basis for identifying old-growth *Juniperus occidentalis* stands, as a prelude to the development of management plans and further research into the functional characteristics of the systems. A definition of old-growth juniper woodlands is presented.

Resumen

Mientras que en el oeste de Estados Unidos se ha dado considerable atención a la expansión aérea del “Juniper” (*Juniperus* sp.), la presencia y el significado ecológico de las comunidades viejas de “Juniper”han sido muy ignoradas. Un aumento en el reconocimiento de estas comunidades ha despertado preguntas acerca de como reconocer el crecimiento viejo, la estructura de la comunidad, la importancia ecológica y el manejo apropiado. Como un análisis inicial de los bosques de viejos del “Western juniper” (*Juniperus occidentalis* Hook var. *occidentalis* Vasek) de la parte central de Oregon este estudio investigó la estructura de la comunidad de crecimiento viejo en suelos arenosos eólicos. Estos bosques representan los mas extensos bosques decrecimiento viejo de “Western juniper” a través de su rango. Se establecieron 9 parcelas de estudio en 7 sitios. Dentro de cada parcela se registraron las densidades y atributos físicos de todos los árboles vivos, de pie y caidos en descomposición. Medidas adicionales tomadas en los árboles vivos fueron: cobertura de la copa, clase de edad aparente (pre o post-colonización) y un muestreo de la edad de los árboles. Estimar la edad de árboles de mas de 250 años fue complicado por la extensiva pudrición del centro del árbol. La densidad de arbustos y la cobertura fueron medidas por especie. La cobertura de la vegetación baja se midió por especie y tipo funcional. También se midieron: el suelo desnudo, rocas, mantillo de “Juniper”, otro tipo de mantillo, musgos y costra criptogamica. La cobertura vegetal vario de 11 a 33% para árboles, de 0 a 10% para arbustos, 3 a 12% para zacates perennes, 1 a 2 % para hierbas y de 0 a 0.1% para zacates anuales. Los bosques contenían al menos 80 árboles ha-$^{-1}$ de una edad de más de 200 años. Las correlaciones entre los parámetros de los arboles y la estructura de la vegetación baja y composición fueron generalmente pobres. Las diferencias en la composición de plantas entre estas poblaciones fueron principalmente atribuidas a la elevación, pendiente y porcentaje de arena contenida en el suelo. Las características estructurales que distinguieron a las poblaciones de árboles viejos de las de arboles nuevos incluyeron la forma de crecimiento de los árboles, la presencia de biomasa muerta y residuos grandes de madera muerta, líquenes en las ramas muertas y una copa relativamente abierta. Los resultados proveen una base preliminar para identificar las poblaciones viejas de *Juniperus occidentalis* como un preludio para el desarrollo de planes de manejo y futura investigación dentro de las características funcionales de los sistemas. Se presenta una definición de bosque de crecimiento viejo de “Juniper”.

Key Words: *Juniperus occidentalis*, structure, pinyon-juniper

In the Intermountain West, it is estimated that 3 to 5%, or nearly 160,000 ha, of western juniper woodland is old-growth (USDI-BLM 1990, Miller et al. 1999). However, attention has primarily

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focused on the rapidly expanding postsettlement stands of juniper throughout the western United States (Miller and Wigand 1994). Resource inventories, management plans, range improvement practices, research, and wildlife habitat evaluations typically have not differentiated between old-growth juniper and postsettlement woodlands.

Kaufmann et al. (1992) and Spies et al. (1988) noted that old-growth conifer communities provide unique, and often irreplaceable biological/ecological values, such as animal and plant habitat, biodiversity and genetic pools, and long-term climate records. The Forest Service has defined old-growth forests as ecosystems distinguished by old trees and related structural attributes. Old-growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics which may include tree size, accumulations of large dead woody material, number of canopy layers, species composition, and ecosystem function (USDA Forest Service 1993). Structural attributes of old-growth are reported to vary with forest type, climate, site conditions, and disturbance regime. Although assessing tree age within a stand is an important index of old-growth development, tree age alone is insufficient for assessing old-growth, even within a species. Structural attributes are more commonly described than functional attributes, due to their relative ease of measurement (USDA Forest Service 1993).

The northern variant of western juniper (*Juniperus occidentalis* Hook var. *occidentalis* Vasek[1]) occupies approximately 3.2 million ha (Bolsinger 1989, Gedney et al. 1999) in southeastern Washington, eastern Oregon, northeastern California, southwestern Idaho, and northwestern Nevada. In the literature, communities typically reported to contain old-growth are described as open juniper shrub savannas occurring on shallow rocky soils or growing along rimrock (Holmes et al. 1986, Miller and Rose 1995). These sites are frequently described as fire-safe because of limited accumulations of understory fuels. However, in the eolian pumice sand region of the Mazama and northwestern edge of the High Desert Ecological Provinces, western juniper old-growth woodlands[2] form relatively extensive stands greater than 100 km^2 and ages of individual trees can exceed 1,000 years. The growth form of old trees is often characterized by a generally nonsymmetrical appearance, rounded spreading canopies, canopies that are often sparse, large irregular tapering trunks, deeply furrowed and fibrous bark, few but heavy branches, and the presence of a bright-green arboreal fruticose lichen (*Letharia* sp.) (Burkhardt and Tisdale 1969, Holmes et al. 1986, Miller et al. 1999). Trees may also support large basal branches and a narrow strip of cambium attached to a single living branch. However, stand structural characteristics including standing and downed dead, decadence of living trees, cavities, and branches covered with lichens have not been quantified for these old-growth woodlands.

The purpose of this study was to define stand characteristics for minimally disturbed old-growth western juniper woodlands in the eolian sand region of central Oregon. Specific objectives were to: (1) quantify overstory and understory structure and composition; (2) determine if structure and composition vary across these woodlands; (3) evaluate the relationship between biotic and abiotic characteristics with plant species composition and structure; and (4) develop a functional definition of old-growth western juniper woodlands in the aeolian sand region of central Oregon.

Study Area

The study was conducted at 7 sites in the eolian sand region in the Mazama and northwestern portion of the High Desert Provinces (Anderson et al. 1998) in central

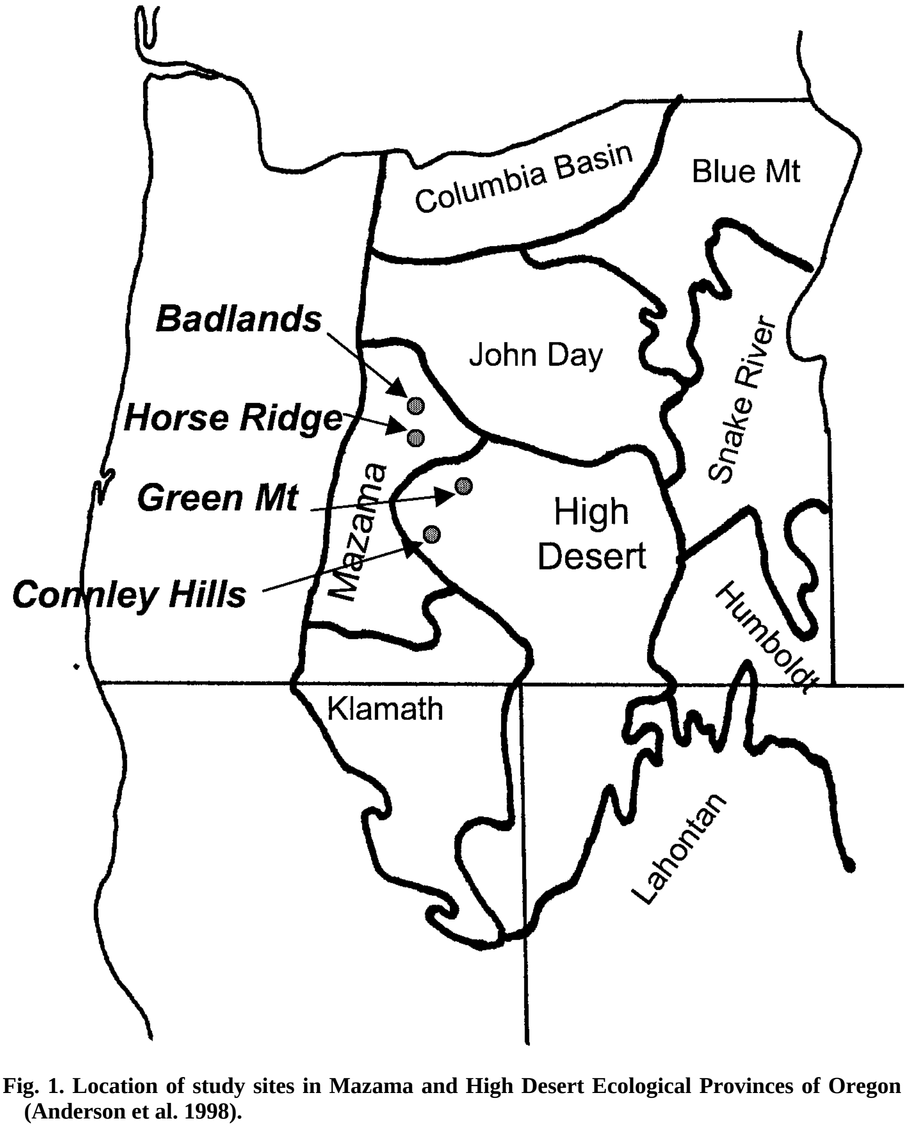

Fig. 1. Location of study sites in Mazama and High Desert Ecological Provinces of Oregon (Anderson et al. 1998).

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[1] Nomenclature follows Hitchcock and Cronquist 1973, and Cronquist et al. 1977.

[2] Woodlands are defined as having a tree canopy cover of ≥ 10%, stands with < 10% tree canopy cover are defined as savannas (Gedney et al. 1999).

Table 1. Study site characteristics. Topographic data are presented as the mean value for the 9 plots at each site. Soils data is based on one or more soil pits dug at each site. Listed plants are western juniper (JUOC), mountain big sagebrush (ARTRV), gray rabbitbrush (CHNA), Idaho fescue (FEID), bluebunch wheatgrass (AGSP), and Junegrass (KOCR).

Site	Connley Hills East	Connley Hills West	Horse Ridge North	Badlands	Green Mtn. North-mounds	Green Mtn. North-interspaces	Green Mtn.
Code	CHE	CHW	HRN	BAD	GMNm	GMNi	GMS
Disturbance	negligible	negligible	negligible	minimal cutting	negligible	cattle grazing,	cattle grazing,
Slope (%)	31	42	17	0	7	3	2
Aspect (°)	95	261	14	0	48	123	174
Elevation (m)	1551	1557	1266	1177	1517	1515	1477
Terrain	steep east slope	steep west slope	north slopes	lava mounds	lava mounds	shallow slope	shallow slope
Soil texture	loamy sand	loamy sand	loamy sand	sandy loam	loamy sand	loamy sand	loamy sand
Soil depth (cm)	75+	67+	60	0+	0 to 42	85	70+
Plant community	JUOC/FEID-AGSP	JUOC/AGSP-KOCR	JUOC/ARTRV /FEID-AGSP	JUOC/ARTRV -CHNA/ AGSP-FEID	JUOC/ARTRV /FEID	JUOC/ARTRV /FEID	JUOC/FEID

Oregon (Fig. 1) between latitudes of 43° and 44° and longitudes of 120° 45' and 121°. Although the Green Mountain and Connley Hills study sites are located in the High Desert Province because of topographic features the pumice sandy soils are similar to those typically found in the Mazama Province. This region supports the most extensive stands of old-growth western juniper woodlands throughout its range (Miller et al. 1999). Seven study sites were located in the 4 largest old-growth stands in this region (Waichler 1998). Two sites were located at Connley Hills, 3 at Green Mountain, and 1 each at Horse Ridge and the Badlands. Two sites were on the north side of Green Mountain; one on rock outcrops and the other between the outcrops. The third site at Green Mountain was located on the south side and did not include rock outcrops. At the Horse Ridge site, plots were located along the apex of 3 adjacent convex ribs of the north slope. At the Badlands site, juniper trees occurred on basaltic lava mounds, or tumuli, that punctuated nearly barren sandy interspaces. Site codes used throughout the remainder of this report (unless otherwise noted) and other information on the sites are shown in Table 1.

Climate in the study area is characteristic of the northern Great Basin. Precipitation has averaged 20 to 28 cm per year, predominantly as winter and spring snow and rain (Taylor 1993). The Natural Resource Conservation Service (NRCS) site description for the Shallow Pumice Hills 25 to 28 cm precipitation zone at Horse Ridge notes air temperatures averaging 8°C annually, with extremes ranging from –32 to 38°C. Soil thermal regimes are frigid, except for a mesic regime in the Badlands.

Soils at all sites were derived from volcanic ash deposits of aeolian origin. Soils typically vary between well drained and excessively well drained (Table 1). Soil on the rock outcrops in the Badlands and Green Mountain North had accumulated in shallow rock depressions. Soils are mapped by NRCS as a complex of Vitrixerandic Haploxerolls (typically 36 cm to bedrock), Lithic Torripsamments, and lava flows (rock outcrop) in the Badlands, Vitritorrandic Haploxerolls (typically 81 cm to bedrock) and rock outcrop on Green Mountain, and Vitrandic Haploxerolls on Connely Hills.

In the central Oregon juniper zone, western juniper is the dominant tree species, with occasional ponderosa pine (*Pinus ponderosa* Dougl.) in favorable locations (Driscoll 1964b). Natural wide spacing of the junipers provides a savanna-like appearance. The most common dominant shrub is mountain big sagebrush (*Artemisia tridentata* subsp *vaseyana* (Rydb) Beetle). Other common shrubs include bitterbrush (*Purshia tridentata* (Pursh) DC.), gray rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britt), green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), and horsebrush (*Tetradymia canescens* DC). In relatively undisturbed communities, bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) and Idaho fescue (*Festuca idahoensis* Elmer) are dominant grasses. Sandberg bluegrass (*Poa sandbergii* Vasey) and Thurber needlegrass (*Stipa thurberiana* Piper) are common. Forbs are not a major constituent of undisturbed communities. Common forbs include buckwheats (*Eriogonum*), wild dandelions (*Agoseris*), locoweed (*Astragulus*), lupine (*Lupinus*) species, yarrow (*Achillea millefolium* L.), rock gilia (*Leptodactylon pungens* (Torr.) Nutt.), and Oregon sunshine (*Eriophyllum lanatum* (Pursh) Forbes).

Methods

Plot layout

Three, 1000 m transects were established within each of the 7 study sites. Transects were systematically laid out to allow complete coverage of each old-growth stand. Three sampling plots were placed on each transect (9 plots per site) except at Green Mountain North where 6 plots were established along each transect, 3 each on and off of the rocky outcrops. Plot locations were selected arbitrarily, but with plots ranging from the first third to the last third of each transect. Plot centers were located by a blind toss of a meter pole. Plot diameters for tree measurements were 20 m. The interspace plots at Green Mountain were located away from the edges of the mounds. At the Badlands site, plots were established on the large lava mounds along each transect. Three, 30 m lines were laid out across each plot. One line was placed through the center of the circular plot, along the terrain contour. The other 2 lines were placed parallel to and 15 m on either side of the center line. At some plots on rocky mounds, adjustments in position had to be made to ensure the entire line was contained on the mound. We made a general search of the area adjacent to each plot for evidence of fire.

Plot measurements

Tree measurements recorded within circular plots were the number of live trees over 1 m tall, standing dead trees (≥ 25 cm diameter at 30 cm above ground level), and large fallen trees pieces. The fallen pieces included full or split tree boles and large limbs (≥ 3.3 m length and 25 cm diameter at large end). Tree heights were estimated using a 3-meter pole placed adjacent to each tree. Trees < 15 cm tall were counted within the 2 x 30 cm shrub plots. Diameters of standing trees were read at 30 cm above ground level using a pole calibrated in 10 cm increments. Fallen piece diameters were measured with a tape measure at 30 cm above apparent ground level. Each live tree within the plot was assigned to a postsettlement (establishing after 1870) or presettlement (establishment prior to 1870) age class based on growth form. Trees placed in the postsettlement age class had symmetrical conical canopies and obvious terminal and lateral leader growth. Presettlement trees had rounded tops and little leader growth. Presettlement trees commonly exhibit deeply furrowed and stringy bark. Additional characteristics may include large lower limbs, dead tops, and strip bark supporting a limited canopy. Live trees were visually placed into a form category based on fullness of the canopy as follows: Form 1—over 90% of the canopy living, Form 2—50 to 90% of canopy live, Form 3—10% to less than 50% of canopy live, Form 4—under 10% of canopy live. Canopy size was measured as foliage spread along and perpendicular to the direction of maximum foliage spread. This technique generally overstates canopy area on trees that do not have a full canopy. On plots where tree cores were collected, an attempt was made to sample all trees. Tree cover was measured using the line intercept method along each 30 m transect (Canfield 1941).

Shrub cover was measured on each 30 m transect using the line intercept method. Both densities of shrubs and juniper trees 30 cm to 100 cm tall were measured in a 2 m wide belt transect centered on each 30 m transect. Live herbaceous, litter, rock and bareground cover were estimated in 30, 0.2 m^2 plots placed at 3 m intervals along each 30 m transect.

One or more soil pits were dug at each site to determine soil depth and texture. Texture was measured for each horizon using the hydrometer method of particle size analysis (Gee and Bauder 1986).

Data Analysis

Data were reduced to means and standard errors by site. Analysis of variance and regression analysis were used to test for relationships between understory attributes with abiotic or tree structural attributes. These analyses were done using the SAS System for Windows, Version 6.12 with a significance level of 0.05 (SAS 1996).

To show the arrangement of the plots based on species composition and allow comparison of the within-site and between-site distribution, ordination was done using the Nonmetric Multidimensional Scaling (NMS) technique (Kruskal 1964, Mather 1976). This iterative technique ordinates based on ranked distances between sites, avoiding the assumption of data normality. "Stress" is used in NMS as a measure of departure from monotonicity in the relationship between the distance between plots in the original many-dimensional space and the distance in the reduced-dimensional space. Analysis was done using PC-ORD for Windows, Version 3.03 (McCune and Mefford 1995). Species diversity indices were also calculated using this program.

Data were first reduced into 2 matrices. A species cover matrix contained the percent cover of each understory species and the tree density for each plot. This measure of tree importance was used because it was the most accurate of the measurements taken and because linear regressions had shown it to have better correlation with environmental parameters than the other tree parameters studied. To reduce the high skew (5.0) and coefficient of variation (460%) in the totals of species, several adjustments were made. Species occurring in fewer than 5% of the plots (fewer than 4 plots) were deleted, leaving 56 species in the matrix. Juniper density data was log transformed. Species cover data was transformed as follows:

transformed value = log (original value + minimum non-zero cover value in matrix) – log (minimum non-zero cover value in matrix).

This transformation allowed initial values of zero to remain zero. The second matrix contained plot environmental data and other plot parameters. This matrix contained slope (degrees), heat load on a scale of zero to one [1 - cos (aspect angle - 45)/2], elevation, species richness, total understory plant cover, tree density, tree basal area, tree canopy area, and ground cover by rock, bare ground, moss, crust, juniper litter, and other litter for each plot.

An initial run was made using 6 dimensional space, Sorensen distance, and 100 iterations. Plots of stress versus iteration were examined for instability and to find the lowest number of axes at which the reduction in stress gained by adding another axis was small. A final run of 100 iterations was made using 3 axes with a randomly selected starting configuration. Monte Carlo simulation was included as a check on whether a similar final stress could have been obtained by chance. The stress obtained with the data set was compared to the stress from 20 runs of randomized versions (data shuffled within columns) of data. Additional runs were compared to ensure that the solution was not at local minima. Overlays of individual species, plant functional types, and environmental variables on the resulting ordination allowed for an examination of the correlation between these variables and the ordination axes.

Results

Woodland structure and composition

Structural attributes among the old-growth western juniper woodlands were summarized for (Tables 2 and 3). Juniper cover averaged 23% (range 11 to 33%), while density averaged 209 live trees over 1 m high ha^{-1} (range 102 to 302). Mean height and diameter were 5 m and 36 cm, respectively. Age of trees < 1 m tall greatly varied in age from recently established trees (< 25 years old) to older trees suppressed.

The majority of woody detritus was retained in standing live or dead trees, with a smaller proportion composed of large pieces on the ground. Standing dead trees and large fallen pieces occurred in the plots at all sites except one. High variability within and between sites occurred for both types of debris. Overall, the mean density of standing dead trees (13 ± 8 trees/ha) was over twice the mean density of fallen detritus (6 ± 14 pieces/ha). Standing dead trees also tended to be larger than the fallen pieces, which could include several pieces from a single tree.

A third component of aboveground woody debris, attached debris such as dead limbs and spires on live trees, was not measured but appeared to be the most prevalent in these woodlands. Lichens (*Letharia columbiana* (Nutt.) J.W. Thomson and *L. vulpina* (L.) Hue) were frequently found on dead wood. One example of attached debris was wood that had been dead for over 600 years (determined by cross-dating) on a 1600-year-old tree found adjacent to a plot on the Horse Ridge North site. A qualitative measure of this component may be provided by the form classes of the trees found at the site. Sixteen percent of live trees (height at least 1 m) in the study plots had canopies less than 50% complete, with many dead branches retained in the leafless portion of the canopy. Another 40% of trees were missing 10 to 50% of the canopy and also retained dead branches.

Table 2. Plant cover (%), species richness, and diversity. Listed shrubs are mountain big sagebrush (ARTRV), gray rabbitbrush (CHNA), green rabbitbrush (CHVI), and bitterbrush (PUTR).

	CHE		CHW		HRN		BAD		GMNm		GMNi		GMS		All sites	
Type of cover or richness	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Herbaceous Plant Cover																
Total understory cover	7	3	12	3	11	2	14	4	12	3	12	4	15	3	12	1
Herbaceous plants	7	3	11	3	6	1	5	1	8	2	9	3	14	3	9	1
Perennial grasses	5	2	9	3	5	1	3	1	7	2	8	3	12	2	7	1
Perennial forbs	1	2	1	1	1	0	2	1	1	1	1	0	1	1	1	0
Annual grasses	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Annual forbs	0.2	0.2	0.5	0.4	0.1	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.2	0.1
Tree and Shrub Cover																
J. occidentalis	33	9	14	7	18	6	11	5	32	9	21	7	31	10	23	2
Total shrub cover	0	0	1	1	6	2	10	4	4	3	3	2	1	1	3	1
Dominant shrubs	none		ARTRV		ARTRV		ARTRV/ CHNA, CHVI PUTR		ARTRV		ARTRV		ARTRV		ARTRV	
Other Ground Cover																
Total other ground cover	93	3	89	5	94	2	96	1	92	2	90	4	84	5	91	2
Rock	39	5	64	8	15	8	37	12	27	11	2	2	3	4	27	3
Bare ground	18	8	5	3	46	8	18	9	24	11	63	9	49	9	32	2
Cryptogamic crust	1	1	1	3	1	1	1	1	1	1	1	1	1	0	1	1
Moss	9	6	1	1	10	3	11	4	12	6	5	4	3	2	7	2
Juniper litter	22	6	13	5	15	5	23	6	23	5	13	6	23	9	19	2
Other litter	5	2	4	3	8	2	6	2	4	2	6	4	5	2	6	1
Species Richness and Diversity																
Shrub species/site	1		4		6		5		5		3		4		7	
Total species/site	49		41		58		44		53		44		40		89	
Simpson index	0.2		0.3		0.2		0.4		0.3		0.4		0.5			
Shannon-Wiener index	9.6		6.5		8.2		5.4		6.6		4.4		4.3			

Shrub cover averaged 3% (range from 0 to 10%). Mean density was 2,829 live shrubs ha^{-1}. Dead shrubs average 869 ha^{-1}. On a site basis, live shrubs constituted between 24 and 73% of all shrubs. The most abundant shrubs were mountain big sagebrush and gray and green rabbitbrush with bitterbrush and horsebrush occurring on more than one site.

Herbaceous vegetation accounted for only 9% (range 5 to 14%) of total ground cover. The majority of ground cover characterizing these stands was predominately bareground, rock, and juniper litter. Perennial grasses dominated the herbaceous layer with 7% mean cover across the sites. Idaho fescue and bluebunch wheatgrass were dominant grasses with junegrass (*Koeleria cristata* (Ledeb.) Schult.), Sandberg bluegrass, squirreltail (*Sitanion hystrix* (Nutt.) Smith), and Thurber needlegrass commonly present. Perennial forbs averaged 1% cover. The most abundant forbs were thread stalk milkvetch (*Astragalus filipes* Torr.), rock gilia, and silvery lupine (*Lupinus argentus* Pursh.) followed by wooly groundsel

Table 3. Woody plant densities and other tree attributes. Densities are given in number/ha.

	CHE		CHW		HRN		BAD		GMNm		GMNi		GMS		All sites	
Shrub or Tree	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.	mean	s.e.
Density Of All Shrubs																
Total live and half live	99	138	574	568	4383	806	9068	3983	2407	836	1988	684	1284	343	2829	1317
Dead shrubs as % of total	68%		29%		14%		21%		26%		30%		41%		24%	
Juniper Densities																
Live trees (at least 1 m tall)	302	96	114	43	258	79	192	61	322	121	102	47	175	50	209	29
Old-growth trees	231	70	88	32	167	68	131	46	235	79	73	36	82	26	144	83
Regeneration																
Seedlings (< 15 cm tall)	0	0	86	155	6	19	37	56	56	167	25	40	0	0	30	70
Juvenile (15–100 cm tall)	2	5	3	4	13	11	22	24	9	16	47	40	26	31	17	13
Detritus																
Fallen dead pieces	17	42	11	8	3	6	3	7	1	3	0	0	7	6	6	14
Standing dead trees	22	19	13	14	9	12	19	19	21	19	0	0	6	5	13	8
Other Live (at least m tall) Treet Attributes																
Basal area (m^2/ha)	21	4	18	4	22	2	22	7	39	11	20	7	24	5	24	3
Mean heigh (m)	5	1	4	1	4	0	4	1	5	0	6	1	6	1	5	0
Mean diameter (cm at 30 cm above ground)	28	5	43	11	30	6	32	4	36	6	47	11	36	7	36	3
% with presettlement form	77%		78%		76%		85%		75%		65%		38%		70%	
Juniper Ratios																
Live trees : 15–100 cm trees	192		43		21		9		34		2		7		12	
Live trees : fallen dead pieces	17		11		82		58		365		n.a.		25		35	
Live trees : standing dead trees	14		9		27		10		15		n.a.		28		16	
Live trees : dead trees or pieces	8		5		21		9		15		n.a.		13		11	
Height : diameter of live trees	17		10		13		14		13		14		16		14	
Old-growth trees : live trees	77%		77%		65%		68%		73%		72%		47%		69%	

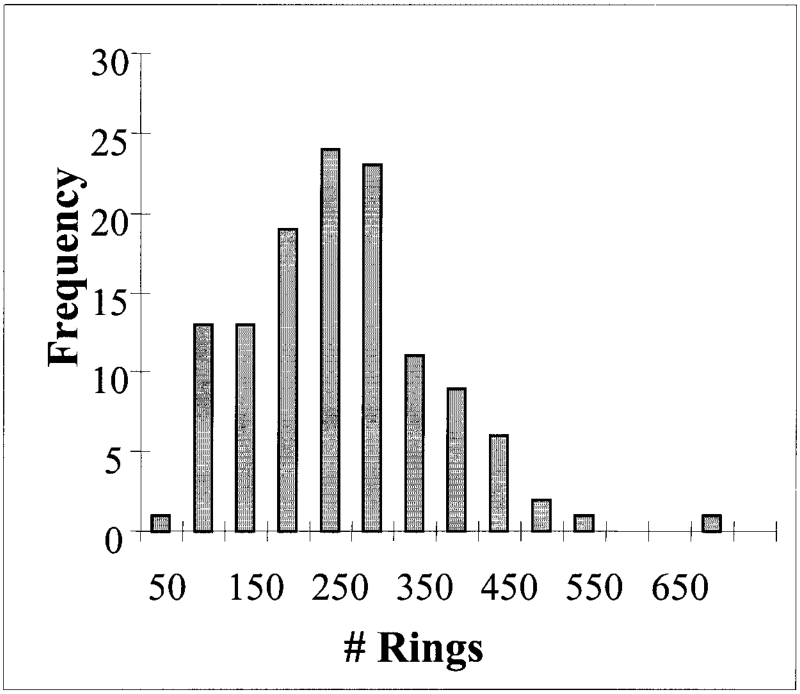

Fig. 2. Growth ring counts of trees sampled in plot. Ring counts are based on incomplete samples for most trees > 250 years due to rot, so ages are underestimated.

(*Senecio canus* Hook.), low pussytoes (*Antennaria dimorpha* (Nutt.) T. & G.), threadleaf fleabane (*Erigeron filifolius* Nutt.), and alkali buckwheat (*Eriogonum strictum* Benth). Annual species cover was less than 1% at all 7 sites. No individual annual species exceeded 0.10% cover at any site.

Plant community diversity was more variable than the number of species found at a site (Table 2). Species richness ranged from 41 to 58 species. At the site level, the Simpson diversity index varied from 0.16 to 0.47, while the Shannon-Wiener index ranged from 4.3 to 9.6.

Tree age and form

Sixty-nine percent of all the trees measured (n = 1132) across the 7 sites were grouped as presettlement based on growth form. Among sites, $\geq$ 65% of trees > 1m in height were presettlement. However, 78% of the successfully cored trees (n = 123) across all 7 sites had more than 130 rings (Fig. 2). Eleven percent of the trees cored, which were classified as postsettlement, had greater than 130 growth rings. Among these 13 trees, 8 ranged in age between 138 and 164 years, 2 between 178 and 192, and 3 between 206 and 250 years. The persistence of conical-shaped canopies in some trees caused us to underestimate the number of presettlement trees using growth form. Across all sites there was a sharp decline in samples collected with greater than 270 rings due to the onset of heartwood rot in the 1730s. This phenomena was reported across a relatively extensive area for western juniper by Knapp and Soule (1999). Trees for which complete or nearly complete cores were obtained had a median ring count of 288 years. This is a highly conservative estimate of the average tree age, as the sample was biased toward younger trees by the difficulty of obtaining complete cores in older trees.

Eighty percent of the trees sampled had over 50% of their leaf canopy still alive, with 31% of the stand having over 90% of their canopies intact. Trees with less than half of their leaf canopy intact accounted for 20% of the stand. Postsettlement trees predominantly had full canopies, with 80% having over 90% of their canopy. Although postsettlement trees had a greater portion of their leaf canopies intact, the percent of live or dead canopy was not a good attribute to separate presettlement and postsettlement trees.

Species Composition

The relationship between understory species composition with other plot attributes, such as soil texture, elevation, and slope, arranged the 7 sites into groups occupying different sectors of ordination space, using 3-dimensional NMS ordination (Fig. 3). The axis numbers were assigned arbitrarily for this figure, since NMS does not arrange axes in order of importance.

Results from ordination were significant (Monte Carlo p-value = 0.05, correlation coefficient for ordination distance and distance in the original 56-dimensional space = 0.83). The Connley Hills, Horse Ridge North, and Badlands sites occupy separate sectors of the ordination space. There was some overlap between the east and west Connley Hills sites. The Green Mountain sites were less distinct, overlapping with the Connley Hills and Horse Ridge. The 2 Green Mountain north sites intermingled and the south site overlapped with the north-interspace site.

Correlation's between species composition and other plot attributes were seen in vectors overlaid on the ordination. The ordination axes were correlated with site topography, ground covers other than vascular plants, species richness, total understory cover, and the tree parameters density, mean height, mean diameter, basal area, and canopy area. Figure 3 shows overlays of vectors for the variables that had correlation coefficients of 0.30 or greater with any axis. The strongest correlation between plant species composition within communities and abiotic parameters were, in declining order, % sand in soil (correlation with Axis 1 = 0.70), elevation (0.59 with Axis 1), % clay in soil (0.53 with Axis 2), slope (0.46 with Axis 1), rock cover (0.45 with Axis 2), and heat load (0.40 with Axis 2). The high correlation of bare ground with community composition (0.36 with Axis 2) likely reflected a combination of cause and effect.

Most tree parameters correlated poorly (correlation coefficient < 0.10) with axes determined from species composition. The exception was tree height (0.48 with Axis 3). This suggests that tree height was responsive to the same environmental factors that affect understory composition. Tree density showed no correlation (< 0.03 with each axis) with understory composition.

Regression analysis showed little relationship between tree parameters and understory composition. Of tree density, cover, basal area, and litter, only density of trees >1m tall had a significant correlation with any understory attributes. An increase of 100 trees ha^{-1} corresponded to a decease of only 1% perennial grass cover (p = 0.0012) and an increase in species richness of 2 (p = 0.0006). This again would suggest that differences in site potential such as soil texture, slope, elevation, and heat load were primary factors determining species composition and cover.

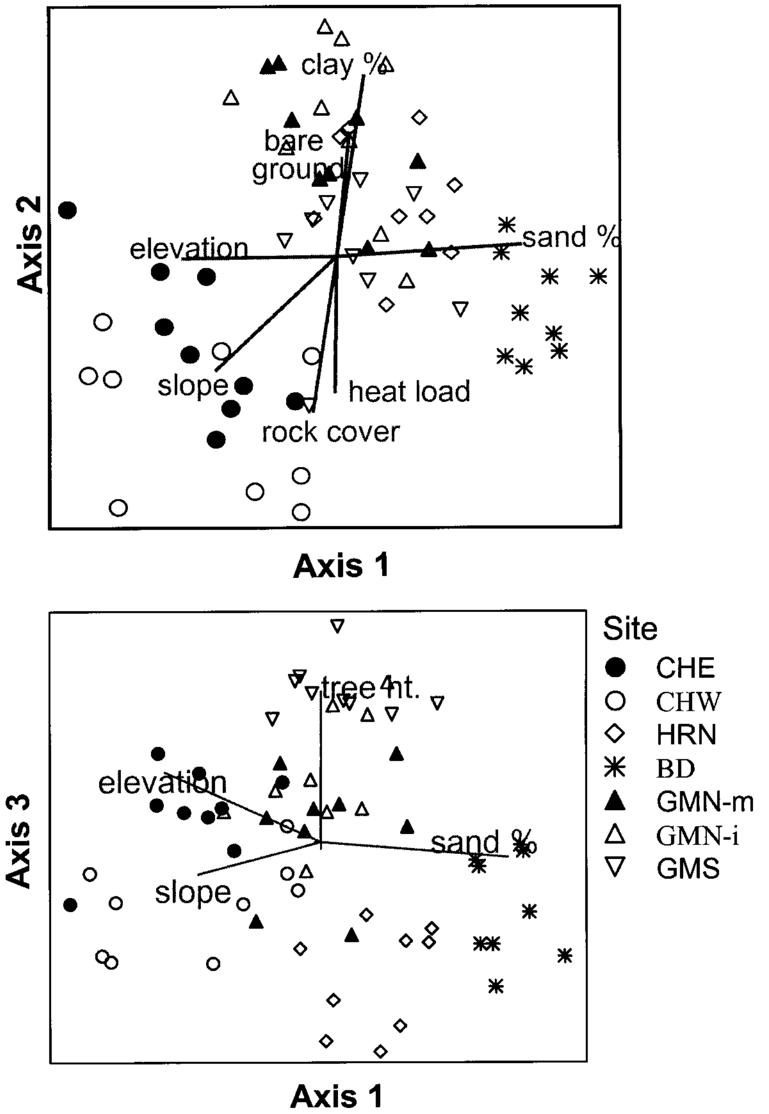

Fig. 3. Arrangement of plots in 3-D ordination space, with overlays of site attributes having 42 > 0.30 or greater with any axis. Vectors are scaled in proportion to r^2. For example, the correlation between elevation and Axis 1 is 0.594 in the negative direction. Loops surround plots by area. Areas are; GRN - Green Mountain North mound (m) and interspace (i); GMS - Green Mountain south, GMW - Green Mountain west, CHE - Connley Hills east and CHW - Connley Hills west, HRN - Horse Ridge north, BD - Badlands.

Numerous individual species responded to the same gradients as the overall communities in the NMS ordination, as shown in Figure 4. Two dominant grasses responded along the clay content gradient, with Idaho fescue showing a strong positive correlation (0.44 with Axis 2) and bluebunch wheatgrass showing a similarly strong, but negative, correlation (0.48). Other species responding to soil clay content were Ross sedge (*Carex rossii* Boott), Thurber needlegrass, cheatgrass (*Bromus tectorum* L.), and broom buckwheat (*Eriogonum vimineum* Dougl.). Mountain big sagebrush increased along with clay and sand content and decreased with increasing slope and elevation. Rock gilia correlated with the sand content gradient. Junegrass and alkali buckwheat correlated positively with elevation and negatively with sand content. Thread stalk milkvetch increased with elevation and slope and decreased with increasing sand content. Compared to these species, correlations of the ordination axes and cover by functional group were weaker. Perennial grass (0.26 with Axis 2 and 0.20 with Axis 3), and annual forbs (0.26 with Axis 1) had the highest correlations.

Discussion

This study provided the basis for development of a quantitative old-growth western juniper woodland description, within the aeolian sand region in central Oregon. Old-growth woodlands in central Oregon contained a minimum density of 80 presettlement trees ha^{-1}. These trees were typically over 16 cm in diameter, contained less than 90% of a full canopy, and exhibited morphological characteristics of old-growth trees. However, 11% of the trees retained the postsettlement growth form with symmetrical conical canopy shapes, several 200 years. Tree canopy cover ranged between 11 and 33% with tree basal areas varying from 18 to 39 m^2 ha^{-1}. Dead wood within the stand was primarily retained as detritus in live trees and as standing dead trees. A minimum of 6 standing dead trees ha^{-1} (25 cm diameter) and 1 large (3.3 m length and 25 cm diameter) downed piece ha^{-1} occurs. Plant structure in these old-growth woodlands was different that nearby postsettlement woodlands described by Driscoll (1964a, 1964b) (Table 4).

Tree parameters generally correlated poorly with understory structure and composition. This may have been due to; (1)

Table 4. Comparison of old-growth *Juniperus occidentalis* communities to earlier seral communities in central Oregon described by Driscoll (1964a, 1964b).

Parameter	Driscoll A The Island	Driscoll B average (range)	Old-growth sites
Juniper cover	10%	12%	23% (11-33%)
Shrub cover	10%	7%	3% (0-10%)
Shrub species	2	≥ 3	4 (1-6)
Perennial grass cover	13%	13%	7% (3-12%)
Perennial forb cover	1%	4%	1% (1-2%)
Annuals cover	2.4%	0.1%	0.2% (0.0-0.6%)
Species richness (total species noted)	32	not noted	47 (40-58)
Bare ground	42%	not noted	32% (5-63%)
Litter cover	31%	not noted	25% (17-29%)

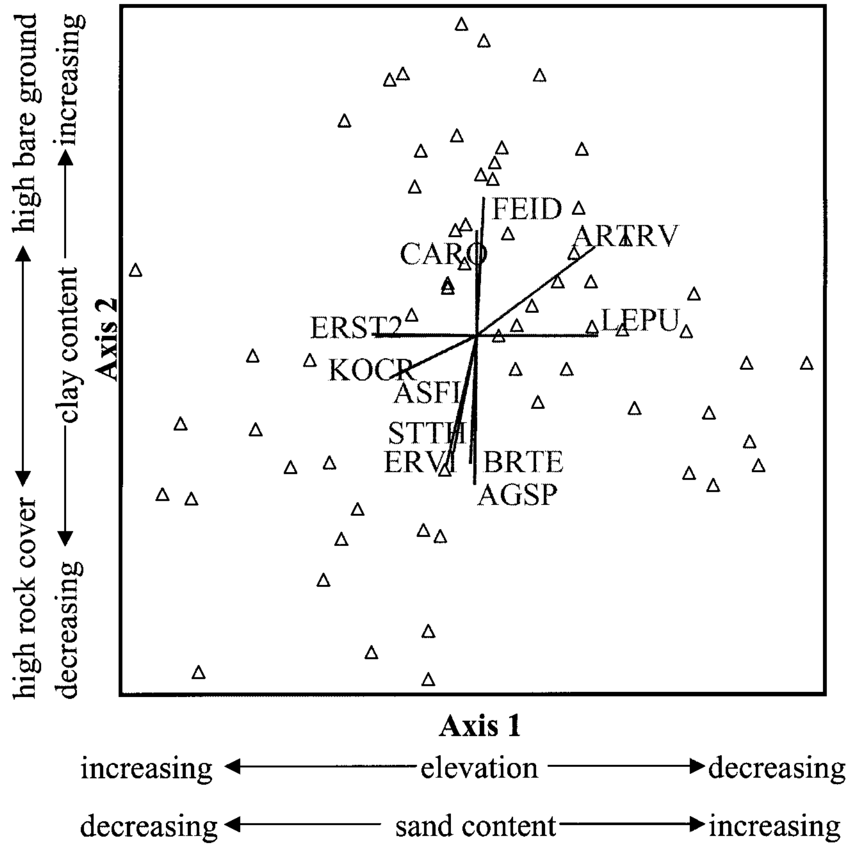

Fig. 4. Overlay of species with highest correlations with ordination axis. Species shown have $r^2 \geq 0.30$ with 1 or more axis. Species shown are *Festuca idahoensis* (FEID), *A. spicatum* (AGS), *Artemisia tridentata* (ARTRV), *Astragalus filipes* (ASFI), *Bromus tectorum* (BRTE), *Carex rossii* (CARO), *Eriogonum strictum* (ERST2). *Eriogonum vimineum* (ERVI), *Koeleria cristata* (KOCR), *Leptodactylon punguns* (LEPU), and *Stipa thurberiana* (STTH). Vectors are sized in proportion to the correlation coefficient, eg $r^2 = 0.479$ for AGSP with Axis 2. Only *Lupinus argentus* and *Antennaria dimorpha* had $r^2 \geq 0.30$ 2 with Axis 3 (both positive correlations).

the limited range in tree canopy cover (11 to 33%) among sites sampled, which was not broad enough to compensate for understory variability, (2) juniper trees were at or near full occupation, or (3) site factors such as soils were more important determinants of herbaceous cover and composition. The low shrub canopy cover (0 to 10%) and tight ring growth of understory trees across most of the study sites indicated stands were in the final stages of woodland development. Miller et al. (2000) reported perennial grass cover did not decrease with increasing juniper cover on deep well drained soils. They also reported low levels of shrub cover in stands approaching the final stages of woodland development where overstory trees dominated the site.

Stand replacement disturbances such as fire appeared not to have played a role in the formation of old-growth woodlands in the eolian sands region of central Oregon. All of the stands we measured were uneven aged, suggesting the absence of a major stand replacement disturbance event. Evidence of fire across the study sites was limited to an individual or grouping of several trees. The presence of old standing and down woody detritus across these sites supports the absence of extensive ground or canopy fires in these communities. Cross dating outer rings of some of this dead material in the Badlands study site indicated death dates varying from 1600 to 1300 AD and establishment dates as early as 0 to 50 BC (unpublished data, University of Arizona Tree Ring Laboratory). The limited role of fire in these old-growth stands is considerably different than more frequent (12-25 year mean fire return intervals) and extensive presettlement fire events reported for mountain big sagebrush communities on igneous soils occupied by rapidly encroaching postsettlement juniper (Houston 1973, Burkhardt and Tisdale 1976, Martin and Johnson 1979, Miller and Rose 1999). The low abundance of fine fuels (grasses and forbs), widely spaced ladder fuels (shrubs), and open tree canopies greatly reduce the probability of low intensity or stand replacement fires in old-growth juniper woodlands occupying the aeolian sands.

Tree canopy cover in these old-growth juniper stands equaled or exceeded the minimum percent canopy of 10% used by the US Forest Service to define woodlands. In the Mazama Ecological Province old-growth stand structure was very different than the widely scattered presettlement trees in stands reported in the High Desert, Klamath, Humboldt, and Snake River Ecological Provinces (Fig. 1) (Holmes et al. 1986, Miller and Rose 1995, 1999). In these provinces old trees are typically found growing on rimrock or low sagebrush (*Artemisia arbuscula* Nutt.)/Sandberg bluegrass tablelands characterized by shallow rocky clay soils and tree canopy cover < 10%. Old-growth was rarely found on sites supporting mountain big sagebrush.

Several distinct differences were noted between our old-growth western juniper stands and those reported for pinyon-juniper communities (Table 5). These descriptions have primarily been developed for the southwestern USA, where the pinyon-juniper definition applies to any mix of the 2 genera, including juniper alone. Western juniper densities among the 7 sites we studied equaled or exceeded the definition developed for pinyon-juniper. Minimum tree basal areas in the plots were also substantially greater in western juniper stands. However, canopy cover and minimum tree diameter were less among the old-growth western juniper woodlands than in the pinyon-juniper. Other live tree parameters were consistent with the pinyon-juniper definition. Woody detritus was more abundant and a greater proportion distributed in standing trees for western juniper woodlands than pinyon-juniper. The average density at all juniper sites was 13 standing dead trees and 6 downed pieces ha^{-1}, while the pinyon-juniper definition specifies 2.5 standing dead and 5 downed pieces ha^{-1}. The abundance of woody detritus may be a function of turnover rate and, or stand age.

Comparison of old-growth western juniper and ponderosa pine provides a sense of how old-growth character can change as a result of local site differences (Table 5). Ponderosa pine occurs in central Oregon in areas with similar elevations and slightly greater precipitation, often overlapping in range with western juniper. The definition of ponderosa pine old-growth developed for Oregon and other USFS Region 6 states, illustrates wide dif-

Table 5. A comparison between *Juniperus occidentalis* old-growth woodlands with old-growth pinyon-juniper (Mehl 1992) and *Pinus ponderosa* (USDA Forest Service 1993).

Parameter	*J. occidentalis* old-growth based on 7 sites	Pinyon-juniper old-growth	Pinus ponderosa old-growth
Old-growth tree density (overstory trees/ha)	80	74	25 trees/ha or 5 trees/ha (late seral)
Minimum diameter	16 cm and ≤ 90% of full canopy	30 cm at root collar	53 cm breast height or 79 cm (late seral)
Minimum age of old-growth trees	200 years	200 years	150 years or 200 years (late seral)
Decadence present	yes	yes	yes (late seral)
Number of canopies	1	1	1
Variation in tree diameters	yes	yes	yes
Minimum tree basal area (m^2/ha)	18	5.3	not specified
Standing dead trees/ha, (minimum diameter	6 (25 cm)	2.5 (25 cm)	7.5 (36 cm DBH)
Down wood pieces/ha, (minimum size)	1 (3 m long, (25 cm diameter at one end)	5 (3m long, 25 cm diameter at one end)	0(1)
Total canopy cover	10–35%	35%	not specified
Understory canopy cover	<20%	not indicated	20–40% typical

[1] The lack of required down wood reflects the natural role of fire in the *Pinus ponderosa* community. Otherwise, typical values are 8 to 15 pieces greater than 2.45 m long and 30 cm in diameter.

ferences in stand structural characteristics in comparison to old-growth juniper. Trees in old-growth juniper are considerably smaller than the old-growth pines, but contain a higher density of overstory trees. The ratio of live old-growth trees to standing dead (standing live:dead) is greater in the western juniper woodland (8.0 versus 3.3). In addition, fallen dead trees are more abundant in the unburned pine forest. This possibly indicates a more rapid turnover of trees in the old-growth ponderosa pine stands.

A distinct contrast between old-growth western juniper woodlands and mesic old-growth conifer forests is the function of woody detritus. Woody detritus appears to function differently in western juniper woodlands than in more mesic old-growth systems. Dead wood is predominantly retained aloft throughout much or all of the decay process, as evidenced by tree boles that have been dead for up to 500 years and dead wood retained on live trees for up to 600 years. In comparison, the estimated time for 95% decay of fallen trees in the Pacific Northwest is 273 years for western hemlock (*Tsuga heterophylla* (Raf.) Sargent) or sitka spruce (*Picea sitchensis* (Bong.) Trautvetter and Mayer) and 429 years for Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Maser and Trappe 1984). Others have reported 3% annual decay rate of coarse woody debris in western Oregon forests (Solins 1982, Spies et al. 1988). Western juniper debris appears to deteriorate more through abiotic weathering than through biotic decomposition. This has a significant, and restrictive, impact on the functions of woody detritus in the old-growth community. Fungal activity appears to be limited. Large fungi were observed on the surface of the wood, but networks of fungal hyphae were not observed in wood in any stage of decay. Arthropods such as carpenter ants were also absent in woody debris across sites. Nitrogen fixation that occurs in moist, well-decayed woody debris in more mesic systems (Franklin et al. 1981) is likely absent or very limited in these more arid systems.

In the study plots, evidence of natural disturbance such as fire, insect infestation, or windstorm was absent or negligible. Anthropological disturbances included a small amount of woodcutting and cattle grazing. These disturbances did not appear to have impacted the structure of the sites.

Defining Old-growth Woodlands

Some of the western juniper woodlands occurring in central Oregon are older than generally believed and are clearly old-growth woodlands. Little has been known about these unique woodlands until now. These ancient woodlands should be identified and mapped so that management plans addressing the special qualities of old-growth can be prepared and implemented. Old-growth trees should be protected from anthropogenic disturbance until their resource values are addressed in management plans. However, criteria for delineating old-growth woodlands have been lacking.

Structural components that characterized old-growth juniper woodlands are easily identifiable. In the absence of major disturbance, structural characteristics including individual tree morphologies typical of old trees, standing and down dead, canopy decadence, abundance of lichen in the tree canopies, hollows, and cavities would be expected to increase over time. Rienkensmeyer (2001) reported cavity nesting birds were 2.7 times more abundant in old-growth than postsettlement juniper stands in central Oregon. These characteristics also distinguish old-growth stands from young post-settlement stands. However, at what point or threshold these characteristics delineate a stand as old-growth becomes subjective since development is a long continuous successional sequence. Criteria used by Woodgate et al. (1996) helps us define old-growth juniper. Using their old-growth model and based on our results we would define a relatively undisturbed old-growth juniper woodland as having; (1) ≥ 75% trees with one or more morphological characteristics expressed by old-growth (rounded tops, furrowed bark, > 10% canopy decadence, strip bark, etc.), (2) <10% regenerating trees in the understory, and (3) <10% of the stand containing cut stumps and recently burned skeletons. Additional structural characteristics that can be used to delineate old-growth woodlands are; ≥ 6 standing dead trees and ≥ 1 down pieces of wood/ha, and lichen in the tree canopies is common (easily seen standing in 1 location). Juniper woodlands containing a predominance of old trees but not meeting the above criteria may reflect stands in earlier stages of old-growth development or locations of different site potentials. The woodlands in this study appeared to have negligible disturbance.

Old-growth juniper woodland characteristics will vary spatially, across soil types and landscape locations, and temporally with stand age. Stand characteristics are highly location specific even within the pumice-dominated soils of this study area. The 7 sites studied differed in structure and composition. Management plans should recognize that such variability occurs within some old-growth woodlands. A full working definition of old-growth western juniper woodlands needs to consider the range of soils where old-growth juniper occurs, plant communities with different understory dominants, and the acceptable limits of natural and anthropogenic disturbance.

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Spatial modeling of rangeland potential vegetation environments

MARK E. JENSEN, JEFF P. DIBENEDETTO, JAMES A. BARBER, CLIFF MONTAGNE, AND PATRICK S. BOURGERON

Authors are ecologist, USDA, Forest Service, Northern Region, Missoula, Mont. 59807; ecologist, USDA, Forest Service, Custer National Forest, Billings, Mont. 59105; ecologist, USDA Forest Service, Northern Region, Missoula, Mont. 59807; associate professor, Land and Environmental Science, Montana State University, Bozeman, Mont. 59715; and research associate, Institute for Arctic and Alpine Research, University of Colorado, Boulder, Colo. 80309-0450.

Abstract

Potential vegetation environments (e.g., habitat types, range sites, ecological sites) are important to land managers because they provide a conceptual basis for the description of resource potentials and ecological integrity. Efficient use of potential vegetation classifications in regional or subregional scale assessments of ecosystem health has been limited to date, however, because traditional ecological unit mapping procedures often treat such classifications as ancillary information in the map unit description. Accordingly, it is difficult, if not impossible, to describe the precise location, patch size, and spatial arrangement of potential vegetation environments from most traditional ecological unit maps. Recent advances in remote sensing, geographic information systems (GIS), terrain modeling, and climate interpolation facilitate the direct mapping of potential vegetation through a predictive process based on gradient analysis and ecological niche theory. In this paper, we describe how a predictive vegetation mapping process was used to develop a 30 m raster-based map of 4 grassland, 5 shrubland, and 6 woodland habitat types across the Little Missouri National Grasslands, North Dakota. Discriminant analysis was used in developing this potential vegetation map based on 6 primary geographic information system themes. Geoclimatic subsections and remotely sensed vegetation lifeform maps were used in predictive model stratification. Terrain indices, LANDSAT satellite imagery, and interpolated climate information were used as independent (predictor) variables in model construction. A total of 616 field plots with known habitat type membership were used as dependent variables and assessed by a jackknife discriminant analysis procedure. Accuracy values of our map ranged from 54 to 77% in grasslands, 62 to 100% in shrublands, and 70 to 100% in woodlands dependent on geoclimatic subsection setting. Techniques are also described for generalizing the 30 m pixel resolution habitat type map to appropriate ecological unit maps (e.g., landtype associations) for use in ecosystem health assessments and land use planning.

Resumen

Los ambientes de vegetación potencial (por ejemplo, tipos de hábitat, sitios de pastizal, sitios ecológicos) son importantes para el manejador de terrenos porque ellos proveen una base conceptual para la descripción de los recursos potenciales y la integridad ecológica. A la fecha, el uso eficiente de clasificaciones de vegetación potencial en evaluaciones de la salud del ecosistema a escala regional y subregional ha sido limitado, esto debido a que los procedimientos tradicionales de mapeo de unidades ecológicas a menudo tratan tales clasificaciones como información secundaria en la descripción de la unidad de mapeo. De acuerdo a esto, es difícil, si no imposible, describir la localidad precisa, el tamaño de parche y el arreglo espacial de los ambientes de vegetación potencial a partir de los mapas mas tradicionales de unidad ecológica. Avances recientes en el área de sensores remotos, sistemas de información geográfica, modelaje de terreno e interpolación de clima facilitan el mapeo directo de la vegetación potencial a través de un proceso predictivo basado en el análisis de gradientes y la teoría ecológica de nichos. En este articulo describimos como un proceso predictivo de mapeo de vegetación fue usado para desarrollar un mapa raster de 30 m de tipos hábitat de 4 zacatales, 5 matorrales y 6 bosques a través de los pastizales nacionales de "Little Missouri"de North Dakota. Se uso análisis discriminante en el desarrollo de este mapa de vegetación potencial basado en 6 temas primarios de sistemas de información geográfica. En el modelo de estratificación predictiva se utilizaron subsecciones geoclimáticas y mapas de formas de vida derivados de vegetación procesada con sensores remotos. Indices de terreno, imagen satelital LANDSAT e información climática interpolada se utilizaron en el modelo como variables independientes (predictivas). Se usaron un total de 616 parcelas de campo con tipo de hábitat conocido como variables dependientes y evaluadas por procedimiento de un análisis discriminate de navaja. Los valores de certeza de nuestro mapa variaron de 54 a 77% en los zacatales, de 62 a 100% en los matorrales y de 70 a 100% en los bosques, dependiendo de la subsección geoclimáticas en la que se encontraban situados. También se describen las técnica para generalizar los mapas de tipo de hábitat de resolución de 30 m por pixel a mapas apropiados de unidades ecológicas (por ejemplo, asociaciones de tipo de terreno) para el uso en las evaluaciones de salud del pastizal y la planeación del uso de la tierra.

Key Words: habitat types, ecological sites, range sites, ecological classification, Geographic Information System, remote sensing, vegetation mapping, ecological units

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Potential vegetation classifications such as ecological sites (RISC 1983), ecological types (USDA, FS 1991) and range sites (Shiflet 1973) are commonly used by land management agencies as a framework for organizing natural resource information, and also as a tool for communicating "natural" baseline conditions for ecosystem health assessments, predictions of vegetation response to management, and resource value potentials. Most potential vegetation classifications utilize indicator plant species to describe environments with similar responses to management. Habitat type (Daubenmire 1968, Pfister et al. 1977, Mueggler and Stewart 1980, Hironaka et al. 1983, Jensen et al. 1988) is an example of a potential vegetation classification system that is widely used by various U.S. land management agencies because relatively few diagnostic species are required to determine a site's ecological potential. In developing habitat type classifications, minimally disturbed, late seral or "climax" plant communities are sampled to determine which combinations of plant species indicate unique environments for management (Pfister et al. 1977). These classifications are, in turn, contrasted with various abiotic components of sampled sites (e.g., soil properties, climate, and geology) to facilitate a better understanding of the complex environments that a habitat type actually represents (Jensen et al. 1990).

Hierarchical ecological unit maps are often used as a basis for the spatial description of potential vegetation (Bailey et al. 1994, Cleland et al. 1997). For example, in the USDA, Forest Service ECOMAP hierarchy (Cleland et al. 1997), the composition of potential vegetation environments is commonly included as ancillary information in the ecological map unit description. Each ecological mapping unit often contains more than 1 dominant potential vegetation type, depending on classification level and mapping scale; hence, this approach commonly does not provide adequate spatial representation of potential vegetation (e.g., patch size, shape, and connectivity) for many land use planning objectives. Consequently, new approaches for directly mapping potential vegetation are now required in most assessments of ecosystem health.

Recent advances in remote sensing, terrain modeling, climate interpolation, and geographic information systems software facilitate such direct mapping of potential vegetation by a process commonly referred to as "predictive vegetation mapping" (Franklin 1995). In this approach, potential vegetation environments are modeled based on mapped environmental variables that are considered to influence vegetation pattern, whether directly or indirectly (Austin and Smith 1989). Predictive vegetation mapping is founded in ecological niche theory and vegetation gradient analysis; it is based on the premises that vegetation distribution can be predicted from the spatial distribution of environmental variables that correlate with or control plant distributions (Franklin 1995).

The primary objective of this paper is to develop a habitat type map using a predictive vegetation mapping process for the Little Missouri National Grasslands of North Dakota. A secondary objective is to illustrate how raster-based maps of potential vegetation (and associated information) can be effectively generalized from 30 m cells to appropriate ecological unit maps, and subsequently used in ecosystem health assessments and land use planning.

Materials and Methods

Study area

This study was conducted within the Little Missouri National Grasslands (hereafter referred to as the Grasslands) of western North Dakota (Lat. 47° 15'N, Long. 103° 30'W), an area of approximately 809,380 ha that is managed primarily by the USDA, Forest Service, for cattle grazing, oil and gas leasing, wildlife habitat, and recreation uses (Fig. 1). These grasslands encompass an area of diverse terrain and vegetation pattern and include 3 subsections (Nesser et al. 1997) of the Northern Great Plains Section (Bailey 1995). The Missouri Plateau Subsection (331 Fd) is characterized by rolling plains, fans, and terraces formed in mixed sedimentary alluvium. Steep to very steep hills, deeply entrenched drainageways, and narrow to wide valley bottom settings formed in residual and alluvial sedimentary materials characterize the Little

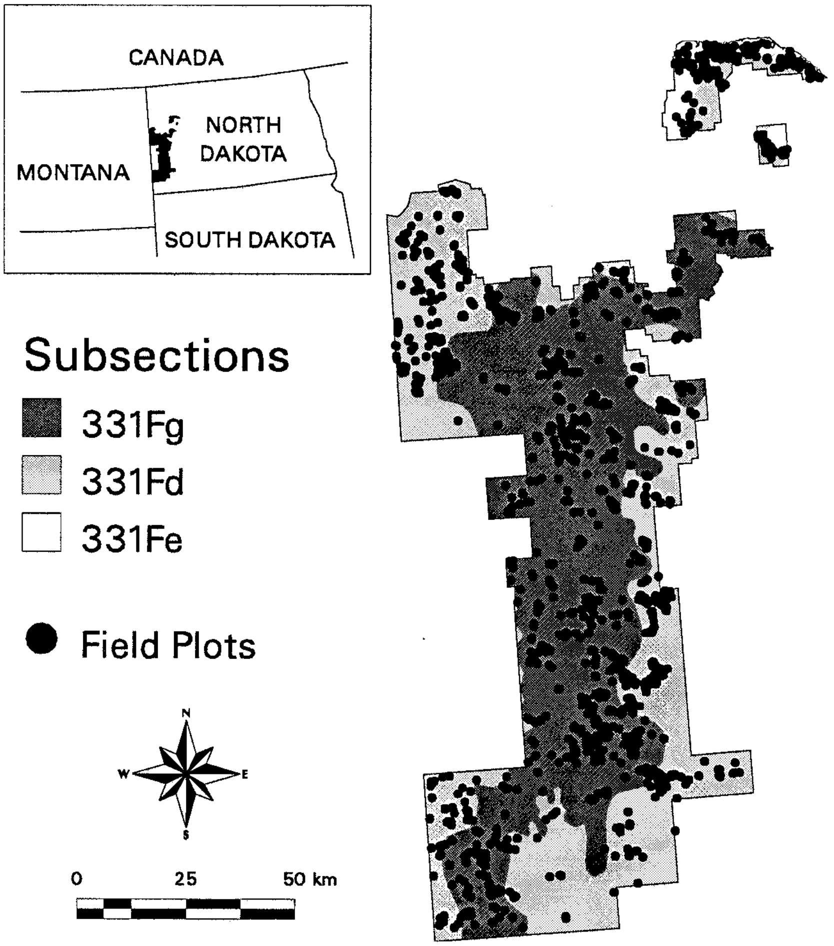

Fig. 1. The study area stratified by geoclimatic subsections and field plots used in describing known habitat type locations within the Little Missouri National Grasslands.

Missouri Badlands (331Fg). The Missouri Breaks Subsection (331 Fe) is characterized by rolling hills, river breaks, terraces and floodplains that formed in alluvium, sedimentary rock, and glacial till materials. Dominant soil great groups (Soil Survey Staff 1975) of the study area include: Haploborolls, Argiborolls, Argiustolls, Natrustolls and Ustorthents (Whitman 1978, Nesser et al. 1997).

The climate of the Grasslands is continental and semi-arid (characterized by hot summers and cold winters). Elevations range from about 350 m along river bottoms to 1,070 m within the Badlands. Precipitation fluctuates annually and seasonally with over 70% occurring between April and September (Whitman 1978). A moisture-temperature gradient exists across the study area from the SW to the NE corners. Along this gradient, average annual precipitation increases from 360 to 410 mm; average annual temperature decreases by 1° C, and the frost free period decreases from 135 to 115 days. A more detailed description of geoclimatic settings within the study area has been developed by the Custer National Forest at the landtype association level (Cleland et al. 1997).

Vegetation of the study area is typical of the mixed grass prairie in the Northern Great Plains. Kuchler (1964) characterized the potential vegetation of this area as a wheatgrass-needlegrass (*Agropyron-Stipa*) association. Dominant species include western wheatgrass (*Agropyron smithii* (Rydb.)), green needlegrass (*Stipa viridula* (Trin.)), needle and thread grass (*Stipa comata* (Trin. & Rupr.)), blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) and threadleaf sedge (*Carex filifolia* (Nutt.). Little bluestem (*Andropogon scoparius* (Michx.)) and prairie sandreed (*Calamovilfa longifolia* (Hook.)) also occur and commonly occupy micro-sites on short slopes and sandy areas, respectively. Various broadleaf and coniferous tree species and shrubs are found on steep north-facing slopes, narrow drainages and draws, and in wide valleys along streams and rivers.

Characterization of field plots

A total of 616 field plots were used to map and describe habitat types in this study (Fig. 1). These plots were sampled by Custer National Forest personnel between 1987 and 1996 for a variety of objectives including: resource inventories, habitat type and seral plant community classification efforts, and ground truth sampling associated with existing vegetation and land cover satellite imagery mapping. Despite the fact that these plots were obtained for different objectives, they all followed standardized field sampling procedures as outlined in the Ecological Inventory and Analysis Guide of USDA, Forest Service, Northern Region (USDA-FS 1988). This facilitated consistent use of field plot data in subsequent analyses. Sampling protocols associated with these field plots are briefly described below.

Field plots were 0.04 ha size and were subjectively located without preconceived bias (Mueller-Dombois and Ellenberg 1974) on representative habitat type settings across the study area (i.e., plots were randomly placed within clearly delineated habitat types). Data collected at each plot included: soil morphology, elevation, geology, landform, landform position, production by lifeform, canopy cover by lifeform, ground cover, canopy cover and plant height by species, and geographic location coordinates (latitude, longitude). Location data were derived from both 1:24,000 topographic maps and global positioning systems (GPS). Accuracy for non-GPS plot positions is within 100 m , and accuracy for GPS data ranges from 1 to 30 m, depending on whether or not data were differentially corrected. The habitat type membership of each plot was determined based on floristic and abiotic characteristics following hierarchical dichotomous classification key structures developed for the study area by Jensen et al. (1992).

Predictor variables

A variety of raster-based climatic, topographic, and satellite imagery variables (Table 1) were associated with each field plot using ARC/INFO Geographic Information System (GIS) software for subsequent use as predictor variables in potential vegetation map construction. Nine climatic variables (Table 1) were calculated for a 200 m grid using a soil-climate interpolation model developed by the USDA, Natural Resource Conservation Service (NRCS) (Waltman et al. 1997). Primary input parameters for this model include: daily temperature and precipitation from local weather stations; soils data from USDA, NRCS, 1:250,000 STATSGO database; and topographic data from a 30 m digital elevation model. The original 200 m climatic grid was re-sampled to a 30 m resolution to relate climate variables with the other predictor variables used in this study.

Six topographic variables (Table 1) were calculated across the study area using a 30 m digital elevation model. Slope aspect was categorized into 3 classes: no aspect (slopes < 5%), high solar aspect (135 to 315 degrees), and low solar aspect (316 to 134 degrees). A terrain shape index (TSI) was calculated following procedures described by McNab (1989), with positive values indicating concave topography (moisture accumulation) and negative values indicating convex topography (moisture depletion).

Table 1. List of raster–based biophysical predictor variables used in potential vegetation modeling.

Variable Symbol	Variable Name
Climatic Variables	
CST_AMDX	Annual Moisture Surplus/Deficient (mm)
CST_BIO5	Biological Window (days when soil above 5 °C)
CST_BIO8	Biological Window (days when soil above 8 °C)
CST_FFPX	Frost Free Period (days)
CST_GDD	Growing Degree Days above 10 °C
CST_MAAT	Mean Annual Air Temperature (°C)
CST_MSDX	Mean Summer Moisture Deficit (mm)
CST_PET	Potential Evapo-transpiration (mm)
CST_SRPG	Soil Rating for Plant Growth
Topographic Variables	
TSI	Terrain Shape Index
Elev	Elevation (m)
Flat	No Solar Aspect Class (Slopes < 5%)
High	High Solar Aspect Class (aspect 135°– 315° and slopes > 5%)
Low	Low Solar Aspect Class (aspect 316° – 134° and slopes > 5%)
Slp	Slope (%)
Satellite Imagery Variables	
MNDVI	Modified Normalized Vegetation Difference Index
TM1	Landsat Thematic Mapper Band 1 (blue, 0.45 – 0.52 µm)
TM2	Landsat Thematic Mapper Band 2 (green, 0.52 – 0.60 µm)
TM3	Landsat Thematic Mapper Band 3 (red, 0.63 – 0.69 µm)
TM4	Landsat Thematic Mapper Band 4 (NIR, 0.76 – 0.90 µm)
TM5	Landsat Thematic Mapper Band 5 (MIR1, 1.55 – 1.74 µm)
TM6	Landsat Thematic Mapper Band 6 (thermal, 10.4 – 12.5 µm)
TM7	Landsat Thematic Mapper Band 7 (MIR2, 2.08 – 2.35 µm)

Table 2. Habitat types denoted with a (x) are those identified in the final discriminant analysis of potential vegetation environments stratified by lifeform (grasslands, shrublands, and woodlands) and subsection.

Habitat Type	Missouri Plateau	Missouri Breaks	Little Missouri Badlands
Grassland Habitat Types			
Agropyron smithii_Stipa comata	X	X	X
Agropyron smithii_Stipa viridula	X	X	X
Agropyron smithii_Stipa viridula–Bouteloua gracilis	X		X
Andropogon scoparius–Carex filifolia			
Calamovilfa longifolia–Carex			
Stipa comata–Carex filifolia	X	X	X
Shrubland Habitat Types			
Artemisia cana–Agropyron smithii	X	X	X
Artemisia tridentata wyomingensis–Agropyron smithii	X		X
Juniperus horizontalis–Andropogon scoparius	X	X	X
Rhus aromatica–Agropyron spicatum			X
Rhus aromatica–Muhlenbergia cuspidata	X	X	X
Sarcobatus vermiculatus–Agropyron smithii			
Woodland Habitat Types			
Fraxinus pennsylvanica–Prunus virginiana			X
Fraxinus pennsylvanica–Symphoricarpos occidentalis	X		X
Fraxinus pennsylvanica/Ulmus americana–Prunus virginiana	X	X	
Juniperus scopulorum–Oryzopsis micrantha			X
Populus deltoides–Juniperus scopulorum			X
Quercus macrocarpa–Prunus virginiana	X	X	

Two geographically distinct LANDSAT Thematic Mapper (TM) images were acquired for the Grasslands and processed for use in this study (Winne et al. Unpublished). Dates associated with these 2 images were June 1993 and July 1994, which were the most recent cloud-free image dates available for continuous coverage of the Grasslands. The 7 sensors of LANDSAT have proven useful to vegetation pattern mapping in previous research (Sabins 1987). In this study, these 7 spectral bands and a MNDVI value were assigned to a 30 m grid (Table 1). The MNDVI value was derived from spectral bands 3, 4, and 5 and has proven effective in distinguishing areas of high versus low biomass production in other studies (Sabins 1987).

Potential vegetation mapping

A potential vegetation map of habitat types for the Grasslands was developed through the following sequential steps: 1) identification of the habitat types to be mapped, 2) delineation of appropriate biophysical strata for modeling, and 3) multivariate statistical analysis and development of potential vegetation model rule sets by appropriate strata.

The 18 habitat types of the Grasslands described in previous classification efforts (Jensen et al. 1992) were initially considered for mapping in this study. Those types appropriate for mapping were identified by considering both the grain size (spatial resolution) of the predictor variables and the patch size of habitat types as they commonly occur across the study area. Given that the spatial resolution of the predictor variables ranged from 30 m to 200 m, we felt that predicting habitat types with average patch sizes of less than 1 hectare would be inappropriate. Accordingly, 3 habitat types that tended to occur in patches of less than 1 ha (DiBenedetto 1998) were not mapped, but treated as inclusions within the remaining habitat types in final map construction. These habitat types included: *Andropogon scoparius-Carex filifolia*, *Calamovilfa longifolia-Carex*, and *Sarcobatus vermiculatus*(Hook.)-*Agropyron smithii* (Table 2).

In predictive vegetation mapping, predictions based on the chosen environmental variables are greatly influenced by the stratification process used in map preparation (Hutchinson 1982). Accordingly, a study area is commonly stratified by appropriate environmental variables prior to multivariate classification and mapping to reduce the potential number of vegetation classes and separate classes that are “spectrally similar” but geographically disjunct (Franklin 1995).

The initial stratification used to predict the distribution of habitat types in this study was based on the 3 subsections (Fig. 1) previously mapped within the Grasslands at a 1:500,000 scale (Nesser et al. 1997). These were selected because they effectively delineated major differences in climate, geology, and landform across the study area, yet they were large enough to contain sufficient numbers of plots for modeling. Although landtype association polygons (mapped at a 1:100,000 scale) represented more refined delineations of geoclimatic settings within the Grasslands, they were not used as strata in habitat type modeling because of insufficient plot sample sizes within individual mapping units.

Lifeform level maps of existing vegetation (i.e., grasslands, shrublands, and woodlands) developed previously for the Grasslands (Redmond et al. 1997) were used for secondary stratification within subsections during development of habitat type map rule sets. Because vegetation lifeform maps were highly accurate (i.e., over 90% accuracy) and most current disturbance processes within the Grasslands (e.g., herbivory, fire) do not change the lifeform conditions of a site, the use of lifeform maps as secondary strata in habitat type modeling was considered appropriate. Assumptions we made in selecting lifeform maps as a secondary strata included the fact that large stand consuming fires within the Grasslands have been effectively removed since homesteading began about 100 years ago (i.e., fire is currently not a major disturbance process). Additionally, herbivory by cattle rarely changes the lifeform status of a vegetation stand (i.e., most woodlands and shrublands maintain their overstory structures despite changes to understory species composition). The resultant 9 strata (3 subsections times 3 lifeforms) and the habitat types modeled within each of these 9 strata are presented in Table 2. An overview of the various GIS themes used in discriminant analysis modeling of potential vegetation at the habitat type level of ecological classification is presented in Fig. 2.

Statistical Analysis

The statistical analysis used in habitat type map construction included 2 steps. First, the stepwise multivariate analysis of variance test of the Statistical Package for the Social Sciences (SPSS) was used to determine which sets of predictor variables best discriminated between the habitat type membership of all field plots within the Grasslands. Second, variables that significantly ($P < 0.01$) reduced Wilks’ Lambda in the above stepwise MANOVA analysis were then used to compute Fisher

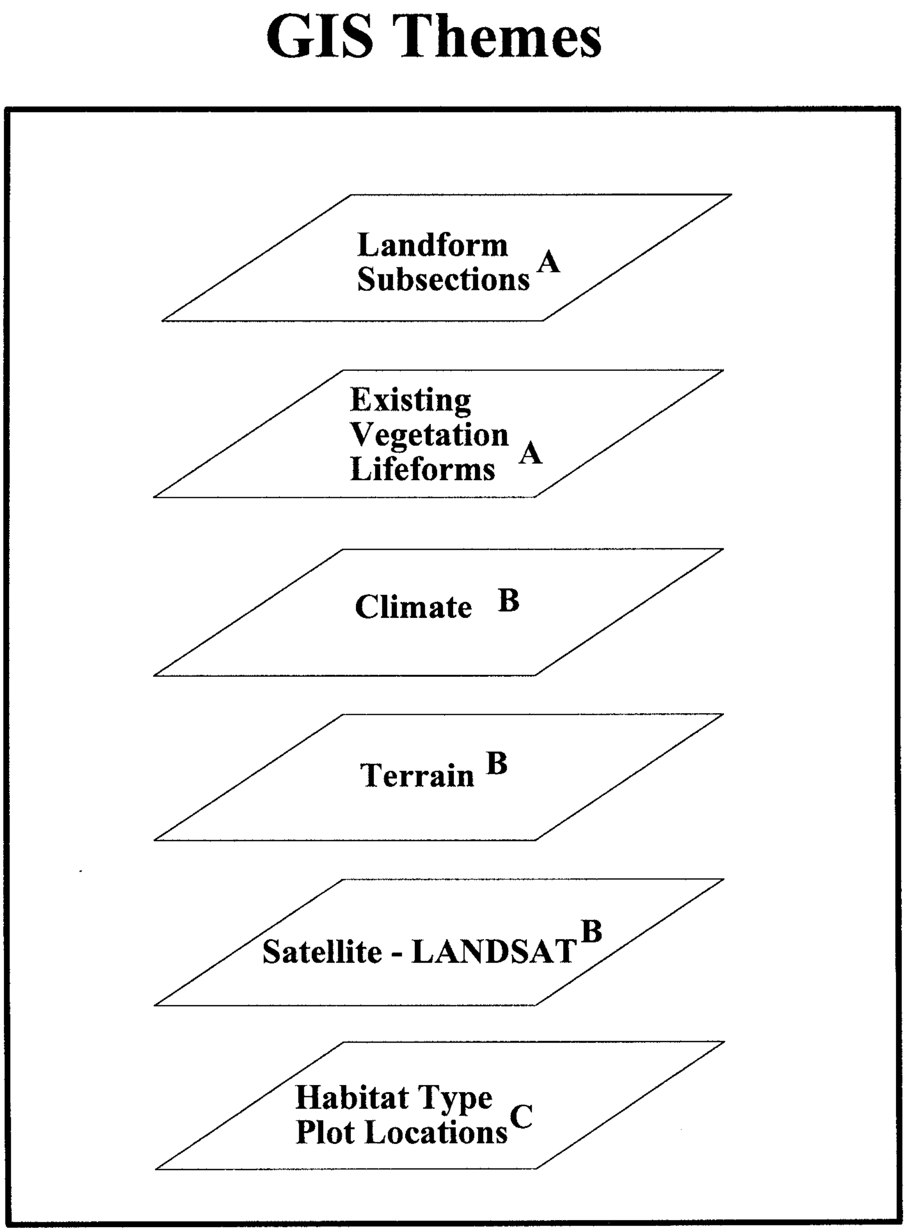

Fig. 2. The 6 basic Geographic Information System data themes used in discriminant analysis modeling of habitat types across the Little Missouri National Grasslands. (A = information used in model stratification, B = information used as independent "predictor" variables in model construction, and C = information used as dependent variables in model construction).

canonical discriminant functions for habitat type prediction by mapping strata. Assessment of the habitat type classification accuracy associated with each of the 9 discriminant analysis strata runs for the Grasslands was determined by a jackknife procedure (Norusis 1985). All plot data were used in developing our habitat type model. We did not split the dataset in our accuracy assessment, because the sample sizes associated with certain habitat types were not adequate once we stratified the data by subsection and lifeform.

The final habitat type map of the Grasslands was registered to a 30 m raster base using Fisher canonical discriminant functions stratified by 9 biophysical environment settings. This map was subsequently generalized to a variety of cartographic presentations based on similarities of predicted habitat type compositions within landtype association and landtype polygons. Clustering of similar polygons was based on Ward's (1963) clustering algorithm in these analyses.

Results and Discussion

Accuracy assessment of the potential vegetation map

An example of our 30 m raster-based habitat type map of the Grasslands developed by discriminant analysis procedures is presented in Fig. 3. Classification accuracy of the complete projection is presented by subsection and lifeform in Table 3, and values are relatively high compared to previous predictions of vegetation pattern by similar discriminant analysis procedures (Franklin et al. 1989, Jensen et al. 1990, Franklin and Wilson 1991, Lowell 1991). Results of this analysis indicate that predictions of habitat types based on biophysical variables (Table 1) were consistently more accurate within woodland (70 to 100%) as opposed to shrubland (62 to 100%) and grassland (54 to 77%) settings across all 3 subsections of the Grasslands. Conversely, accuracy for habitat type predictions across all lifeforms was highest in the Missouri Breaks, followed by the Missouri Plateau and the Little Missouri Badlands subsections (Table 3). These results support the use of environmental stratification for predictive vegetation mapping. Further support was offered by an initial discriminant analysis of habitat types across the Grasslands that was stratified by the 3 lifeforms described above but by only 1 geoclimatic setting (i.e., the Northern Great Plains section). Results of that analysis (DiBenedetto 1998) indicated a habitat type classification accuracy rate of only 20, 32, and 54%, respectively, for grassland, shrubland, and woodland lifeforms across the study area. Stratification of Fisher discriminant mapping functions by subsections (geoclimatic settings) greatly improved the accuracy of predicted habitat type distributions in this study.

Significance of biophysical environment predictor variables in discriminating habitat type patterns

The climatic, topographic, and spectral variables listed in Table 1 were analyzed by a stepwise MANOVA to determine which variables best discriminated between the habitat type membership of field plots and, therefore, should be used in developing Fisher canonical discriminant functions for habitat type mapping. Results of this analysis are presented in Table 4,

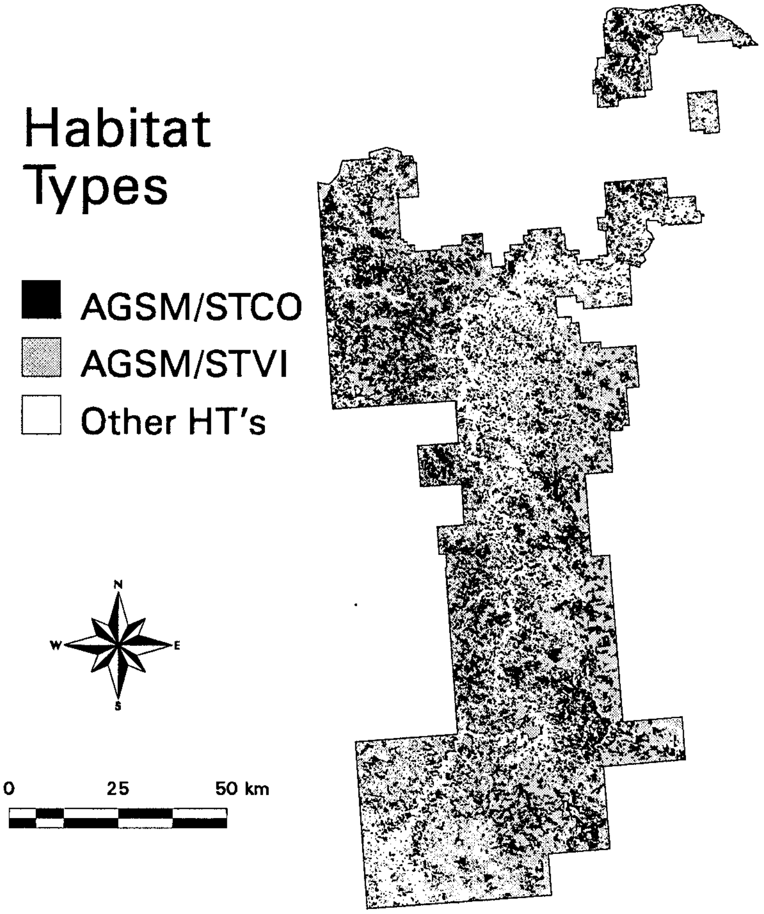

Fig. 3. A 30 m raster-based projection of 2 dominant grassland habitat types across the Little Missouri National Grasslands. (AGSM = *Agropyron smithii*, STCO = *Stipa comata*, and STVI = *Stipa viridula*).

which displays by subsection/lifeform strata, those predictor variables that significantly ($P < 0.01$) reduced Wilks' Lambda and were, in turn, used in Fisher canonical discriminant function calculations.

An examination of the top 3 predictor variables within each column of Table 4 (i.e., those in bold print) suggests that subsections are useful strata in habitat type prediction because they partition the landscape into units that have different predictor variable relations at the lifeform level. For example, within the grassland habitat types, the top 3 predictor variables are different between each of the subsections studied. Variables CST_PET, Flat, and TM5 were the best predictors of grassland habitat types within the Missouri Plateau subsection; however, variables ELEV, CST_FFPX, and MNDVI were the best predictors in the Missouri Breaks subsection, and variables TSI, CST_MAAT, and TM6 were the best predictors in the Little Missouri Badlands subsection (Table 4). Shrubland habitat types exhibit this same relation, with different rankings for the top 3 predictor variables among subsection groupings. Only within the woodland habitat types did the top 3 predictor variables display some commonality between subsections (i.e., CST_PET and SLP).

Lifeform-based stratifications of the Grasslands were also useful in habitat type prediction because they effectively partitioned subsections into units that have different predictor variable relations. For example, within the Missouri Plateau subsection only the variables CST_PET and SLP were within the top 3 predictor variables across 2 or more lifeforms. Similarly, only the variable CST_MAAT was shared as a top predictor between lifeforms within the Little Missouri Badlands subsection, and none of the top 3 predictor variables were shared between lifeforms within the Missouri Breaks subsection (Table 4). These results indicate that the environmental stratification process used in this predictive vegetation mapping study of the Grasslands (i.e., partitioning by subsection and existing vegetation lifeform settings) was effective in habitat type prediction as indicated by the classification accuracy values presented in Table 3.

Consistently higher accuracy within woodlands, followed by shrublands and grasslands, across the 3 subsection strata (Table 3) suggests that the predictor variables used in model construction (Table 1) are reasonable indicators of available soil moisture. This interpretation is supported by previous habitat typing efforts within the Grasslands, in which all researchers concluded that woodlands occupied the most mesic sites, followed by shrublands and grasslands in decreasing order of available soil moisture (Hansen et al. 1984, Hirsh and Baker 1984, Girard et al. 1989, Jensen et al. 1992). Accordingly, it appears that available soil moisture is the primary factor influencing habitat type distribution across the Grasslands. A secondary factor considered important in determining habitat type distribution patterns across the Grasslands is available soil nutrients. This factor is associated with soil types; unfortunately, these were unavailable in digital format and could not be included in this study. Consequently, the broad-level subsection environments of the Grasslands (which were primarily mapped based on differences in landform and surface geology) were the best correlates for soil patterns and associated soil nutrient and waterholding capacities. Observed soil patterns across the Grasslands are most complex within the Little Missouri Badlands followed by the Missouri Plateau and Missouri Breaks

Table 3. Overall classification accuracy of Fisher canonical discriminant functions in predicting the habitat type membership of field plots by subsection and lifeform strata groupings. Accuracy is expressed as the percent of sites correctly predicted within each lifeform and subsection group. "N" is the number of field plots used in modeling potential vegetation environments within each group.

Subsection	Grassland Habitat Types	Shrubland Habitat Types	Woodland Habitat Types
	(%)	(%)	(%)
Missouri Plateau	66; N = 86	88; N = 57	90; N = 31
Missouri Breaks	77; N = 62	100; N = 15	100; N = 41
Little Missouri Badlands	54; N = 97	62; N = 69	70; N = 158

Table 4. Stepwise multivariate analysis of variance listing of biophysical predictor variables that best discriminated between habitat types within the Little Missouri National Grasslands (All of the Wilk's Lambda values presented are highly significant (P< 0.01), with larger numbers indicating those variables that best discriminated habitat type membership of field plots.) Results are presented by the nine subsection/lifeform strata groupings used in developing Fisher Canonical Discriminant Functions for habitat type mapping. Variable symbols are described in Table 1.

	Missouri Plateau			Missouri Breaks			Little Missouri Badlands		
	Grass-lands	Shrub-lands	Wood-lands	Grass-lands	Shrub-lands	Wood-lands	Grass-lands	Shrub-lands	Wood-lands
Climate Variables									
CST_AMDX		0.08			**0.43**			0.17	0.31
CST_BIO5		0.11	0.05		**0.24**			0.28	
CST_BIO8		0.13		0.24	0.03	0.12 .		25	
CST_FFPX	0.26	0.09		**0.36**					
CST_GDD	0.28					**0.29**		**0.32**	
CST_MAAT			0.12			0.11	**0.76**		**0.52**
CST_MSDX									
CST_PET	**0.42**		**0.34**			**0.38**			
CST_SRPG	0.24	**0.33**					0.64		0.29
Topographic Variables									
TSI	0.22		**0.21**				**0.86**	**0.20**	
Elev		0.26		**0.50**		0.14			0.35
Flat	**0.36**						0.56		
High			0.10		0.06 .			015	
Low		0.16							
Slp		**0.56**	**0.50**						**0.66**
Satellite Imagery Variables									
MNDVI	0.30		0.07	**0.30**		0.19			**0.44**
TM1		**0.41**							
TM2						**0.22**			
TM3				0.26			0.60		
TM4		0.20							
TM5	**0.33**							**0.24**	0.38
TM6						0.16	**0.69**		
TM7								0.13	

subsections. As a result, it is not surprising that habitat type predictions were poorest within the Little Missouri Badlands subsection (Table 3).

Management applications

The 30 m habitat type grid produced in this study provides a valuable base map for land use planning because it can be used to describe potentials for resource use, plant community succession pathways, and reference conditions associated with minimally altered ecosystem states (Jensen et al. 1991). Management, however, does not occur at the level of individual 30 m cells. Thus, to facilitate effective use of such base maps in land use planning, they can be associated to appropriately scaled mapping units such as ecological units or multiscale drainage basins depending on specific planning needs (Jensen et al. 1996, 1997). In the following discussion we present some examples of how the habitat type map developed in this study can be effectively generalized to different ecologically based mapping units for a variety of land management uses.

An example of a generalization of our habitat type map for general planning purposes is provided in Figure 4. This map was created by attributing the percent composition of predicted habitat types to each of the Natural Resource Conservation Service soil polygons within the Grasslands, and then clustering these polygons into similar groups based on habitat type composition. The 4 cluster groupings presented in Figure 4 provide a generalization of habitat type patterns across the Grasslands useful to broad-level planning efforts (e.g., forest plan revisions or regional scale ecological assessments). For example, Cluster 1 delineates broad valley bottom settings dominated by woodland and mesic shrub communities. Rolling prairie environments with a predominance of grassland habitat types are displayed in cluster groups 2 and 3. The highly dissected badland environments of the Grasslands are represented by Cluster 4.

Spatial projections of resource value potentials and condition are also facilitated by potential vegetation maps, and are illustrated for year long cattle-forage production potential in Figure 5a. This example was developed based on data collected for reference site (minimally disturbed) plots, which were summarized to describe various late seral plant community characteristics by habitat type (see Jensen et al. 1992). Weighted averages of these values based on habitat type composition within each soil polygon were then calculated by lifeform and across all lifeforms to develop the map presented in Figure 5a. The low, moderate, and high class ratings displayed in Figure 5a are based on average soil polygon values with high values indicating the upper 33% of polygons (>384 kg/ha), low values indicating the lower 33% of polygons (< 244 kg/ha) and moderate values indicating the middle 33% of polygons (244 to 384 kg/ha).

A similar summarization process to that described above was used in estimating the current condition of yearlong cattle-forage production across the Grasslands (Fig. 5b). In this example, ratings were based on the percent similarity between current (from existing vegetation maps) and reference conditions (from potential vegetation maps) and ranged between 24% and 136%. The low, moderate, and high class ratings displayed in Figure 5b are also based on average soil polygon values; and the percent similarity to reference condition values associated with these three classes are 24% to 61%, 62% to 98%, and 99 to 136 , respectively. Ratings of greater than 100% for forage condition occurred because some areas within the Grasslands have been converted from native prairies to crested wheatgrass communities (*Agropyron cristatum* (L.)(Gaertn.)), which commonly have higher forage production values than native reference communities. For a more complete discussion concerning the use of ecological classifications in broad-level assessments of rangeland health and condition, the reader is referred to Jensen et al. 2000.

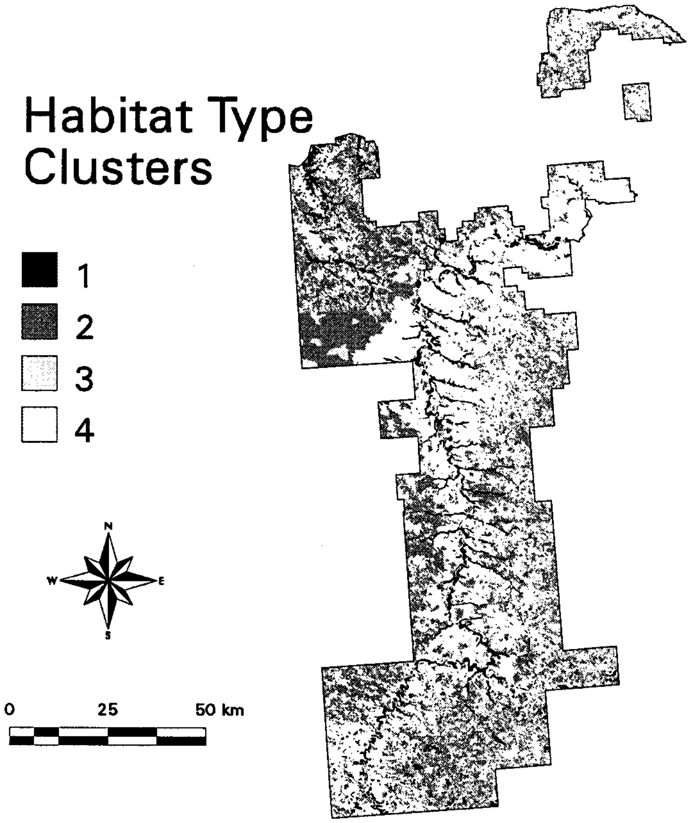

Fig. 4. Generalized habitat type cluster groupings of the Little Missouri National Grasslands appropriate to regional and subregional scale ecological assessments and land use planning.

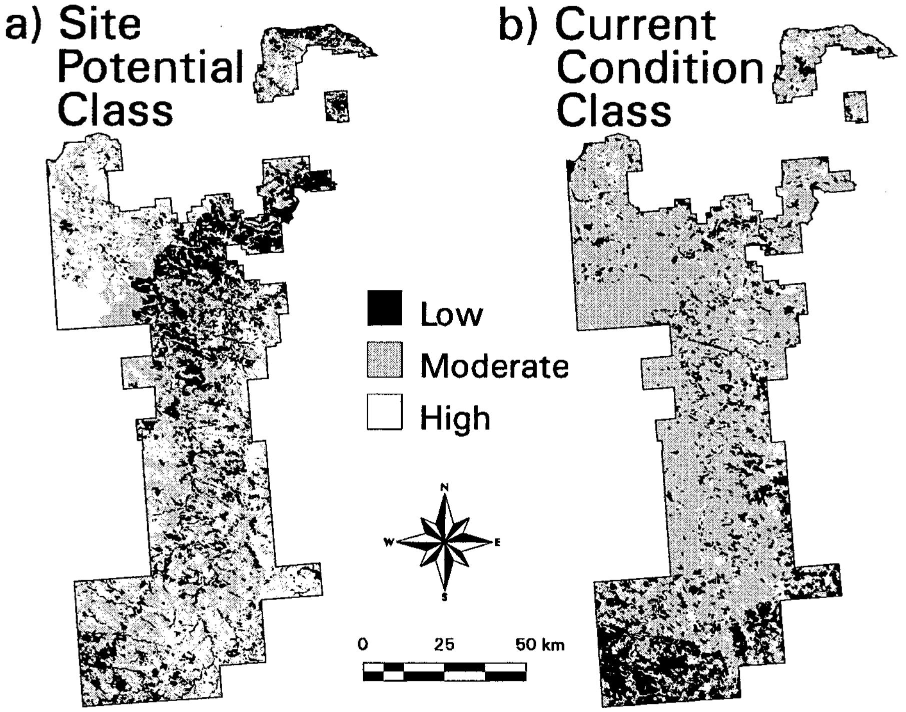

Fig. 5. Year long cattle forage production class ratings for the Little Missouri National Grasslands. (a = site potential ratings based on reference conditions, b = current condition ratings based on the degree of similarity between existing and reference conditions)

Conclusions

The discriminant analysis procedure used to model potential vegetation environments in this study was very effective in predicting habitat types; however, the large number of observations (i.e., field plots) required in this type of analysis might limit its use in other areas. Depending on the number, spatial distribution, and quality of field plot data, as well as the types and spatial resolution of mapped predictor variables available for a study area, a variety of other techniques also can be used in predictive vegetation mapping (see Franklin 1995 for a thorough review). Examples of these other modeling approaches include: Boolean logic, simple regression, multiple regression, logic regression, classification trees, neural networks, simple rule-based methods, and fuzzy logic. Each of these methods have characteristic strengths and weaknesses and may or may not be appropriate to a particular mapping effort given data availability, software limitations, and the personal experience of the research analyst. Regardless of the approach used in predictive vegetation mapping, we offer the following key points that should be considered in future efforts:

- Ensure that the vegetation patterns to be predicted are appropriate given their characteristic range of landscape patch sizes and the grain size of the predictor variables used in modeling (e.g., grain should be 5 to 10 times smaller than average patch size).
- Stratification of a study area into more homogeneous environments greatly improves the performance of a predictive vegetation model.
- When possible, the biophysical variables considered for inclusion in a predictive vegetation model should be tested at multiple spatial scales to determine the appropriate grain size for such information. For example, climate interpolation models (Thornton et al. 1997, Waltman et al. 1997) can be run at 30 m, 90 m, and 1 km resolution to access the spatial scale at which different climatic attributes influence the pattern of interest.
- Gradient-oriented field sampling (Austin and Heylingers 1991, Austin et al. 1994,

Bourgeron et al. 1994) should be used in plot selection to facilitate direct testing of assumed relations between biophysical variables and vegetation patterns.

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Characterization and habitat preferences by white-tailed deer in Mexico

JOAQUIN BELLO, SONIA GALLINA, AND MIGUEL EQUIHUA

The authors are a graduate student, Programa de Ecología y Manejo de Recursos Naturales (Ecology and Natural Resource Management Program); Full Researcher, Departamento de Ecología y Comportamiento Animal (Department of Animal Ecology and Behavior); Full Researcher, Departamento de Ecología y Conservación de Ecosistemas Templados (Department of Ecology and Conservation of Temperate Ecosystems); all at the Instituto de Ecología, A.C., km 2.5 Carretera Antigua a Coatepec, #351, Congregación el Haya, A.P. 63 Xalapa 91070, Veracruz, México.

Abstract

We analyzed the habitat preferences of white-tailed deer in a 1,000 ha area in an arid region of northeastern Mexico where drinking water is abundant throughout the year (via 33 water troughs). Seven habitat types in the study area were identified and characterized. Within each habitat, feeding, searching, and bedding activities were evaluated during the reproduction, postreproduction and fawning seasons of the annual deer cycle. The *Acacia-Celtis* habitat provided the greatest amount of hiding and thermal cover and edible food. The *Prosopis* habitat also provided significant hiding and thermal cover. *Hilaria* and *Opuntia* were the most open habitats. Habitat preferences, evaluated by radiotracking 14 deer over a period of 2 years, varied between sexes and years ($P << 0.00001$), but not among seasons ($P > 0.05$). Male deer preferred open habitats, while females preferred more densely covered ones. Males and females avoided *Prosopis* during 1996. Both sexes distributed the 3 activities more evenly during 1996 than during 1995. In 1995, females preferred *Flourensia* and *Acacia-Celtis* habitats for all activities, and during 1996 males preferred *Hilaria* and *Leucophyllum*. Between year changes in precipitation could explain the observed variability: during 1995 rainfall was 136 mm, as compared to 276 mm in 1996. Requirements for cover increased markedly in 1995 due to high predation and extremely dry conditions. Overall, our study shows that under good weather conditions, habitat preferences are best explained by variables associated with food availability, while thermal cover is more important under harsh weather conditions, even when drinking water is abundant.

Key Words: *Odocoileus virginianus*, Northeastern zone, water sources, radiotelemetry, hiding cover, thermal cover, forage.

Resumen

Analizamos las preferencias de hábitat del venado cola blanca en un área de 1,000 ha, de la región árida del Noreste de México donde el agua para tomar es abundante todo el año (33 bebederos). Fueron identificados y caracterizados los siete tipos de hábitat de la zona de estudio. Dentro de cada hábitat, las actividades alimentación, búsqueda y descanso, fueron evaluadas durante las 3 épocas del ciclo anual del venado: reproducción, postreproducción y crianza. El hábitat de *Acacia-Celtis* tuvo los valores más altos de cobertura de protección y térmica, así como de alimento disponible. El hábitat *Prosopis* tuvo valores altos de cobertura térmica y de protección. *Hilaria* y *Opuntia* fueron los hábitats más abiertos. Las preferencias de hábitat, evaluadas mediante radiotelemetría de 14 venados durante un período de 2 años, variaron entre sexos y años ($P << 0.00001$), pero no entre épocas ($P > 0.05$). Los machos prefirieron los hábitats abiertos y las hembras los de cobertura más densa. Machos y hembras no prefirieron la vegetación de *Prosopis* durante 1996. Ambos sexos distribuyeron de manera más uniforme sus actividades durante 1996 en comparación con 1995. En 1995, las hembras prefirieron para todas sus actividades a los hábitats de *Flourensia* y *Acacia-Celtis*, y en 1996 los machos prefirieron a *Hilaria* y *Leucophyllum*. Los cambios entre años en la precipitación pueden explicar la variabilidad observada: durante 1995 la precipitación fue de 136 mm, en comparación con los 276 mm en 1996. Los requerimientos de cobertura se incrementaron en 1995 debido a la alta depredación y las condiciones extremas de sequía. Nuestro estudio demuestra que en condiciones ambientales buenas, las preferencias de hábitat son mejor explicadas por las variables relacionadas con el alimento disponible, mientras que la cobertura térmica aumenta su importancia en condiciones ambientales extremas, a pesar de la alta disponibilidad de agua.

White-tailed deer (*Odocoileus virginianus*) are selective foragers and prefer habitats with plants that meet their nutritional requirements. Additionally, to decrease the risk of predation and dehydration under extreme conditions, deer select habitats based on the degree of cover (Bleich et al. 1997, Bowyer et al. 1998). When temperatures are high and water scarce, deer use habitats with high thermal cover, which can minimize water loss (Bowyer et al. 1998). However, Boroski and Mossman (1996) mentioned that when water distribution is adequate, the distribution of deer is probably determined by other factors in their environment. The importance of water sources for deer in arid environments (Davis 1990) and the close association between vegetation cover and the presence of water under dry conditions, make it difficult to detect other factors that may affect habitat preference by deer. Studies conducted where water availability is high and constant may further our understanding of other factors important in habitat selection by deer in arid environments.

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Habitat use in arid environments has been studied from various perspectives: presence-absence by habitat, use-availability analysis (Fox and Krausman 1994), comparison of habitats on a usage gradient, according to structural differences (Bowyer et al. 1998), and in the context of management practices (Rollins et al. 1988). Beier and McCullough (1990) considered the activity of individuals and habitat use simultaneously and found diel shifts in habitat use by season. A study of habitat preference in conjunction with tracking individual animal's behavior would help us understand how individual requirements can influence habitat use, however little research has been done from this perspective.

Several studies (Ockenfels et al. 1991, Boroski and Mossman 1996, Rosenstock et al. 1999) have mentioned that habitat preference is influenced by water availability. Our goal was to characterize 7 different habitats and record the preferences and activities of white-tailed deer (*O. v. texanus*, Mearns 1898) by season, sex, and year, in each habitat type on a ranch with high water availability. With 3.4 water sources km^{-2}, the San Francisco Ranch in Nuevo Leon, Mexico, provided the opportunity to explore the importance of other factors that may affect habitat use by deer when water is abundant. We tested the following hypothesis: When water availability is high, habitat preferences are determined by the availability of food and cover provided by the vegetation. We predicted that deer prefer habitats with sparse thermal cover but plentiful food and that deer avoid zones with good thermal cover, but low available food, even during the driest periods.

Methods

Study Area

This research was carried out on the San Francisco Ranch (27° 20' N, 100° 36' W), property of Ducks Unlimited of Mexico, A.C. (DUMAC), located between the municipalities of Lampazos, Nuevo Leon and Progreso, Coahuila, in northeastern Mexico (Fig.1). The ranch covers 1,500 ha, 1,000 of which are enclosed by a 2.4 meter high fence, the only purpose of which is to keep the deer in. An intensive water management program (3 ephemeral streams with dams and 32 water troughs) operate in the enclosed area: the average distance between these water sources is 400 m (3.4 sources km^{-2}). The average elevation of the area is 430 m, with a fairly flat topography and slopes that vary between 3 and 8°. The climate is semi-arid, with a mean annual temperature of 21°C. On occasion, the maximum temperature exceeds 40°C. Annual rainfall averages less than 400 mm (Fig. 2), with notable variations in both monthly and total annual rainfall. The rainy season lasts from May to September. There are few cattle on the ranch, approximately 20–30 head which are rotated and kept within the fenced 1,000 ha for short periods of time.

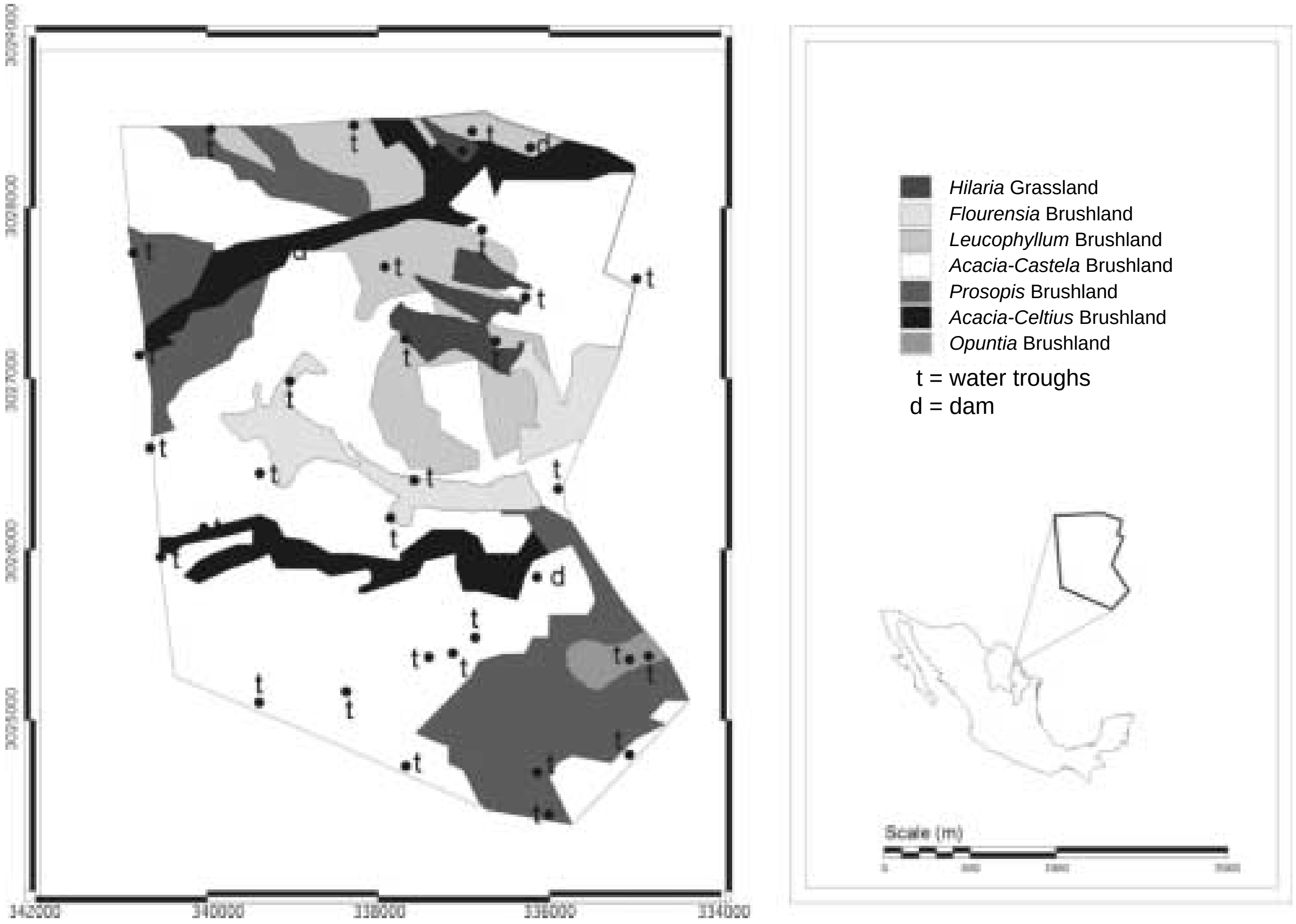

Fig. 1. Location of the San Francisco Ranch, Mexico and map of vegetation associations. Classification modified from Briones (1984)

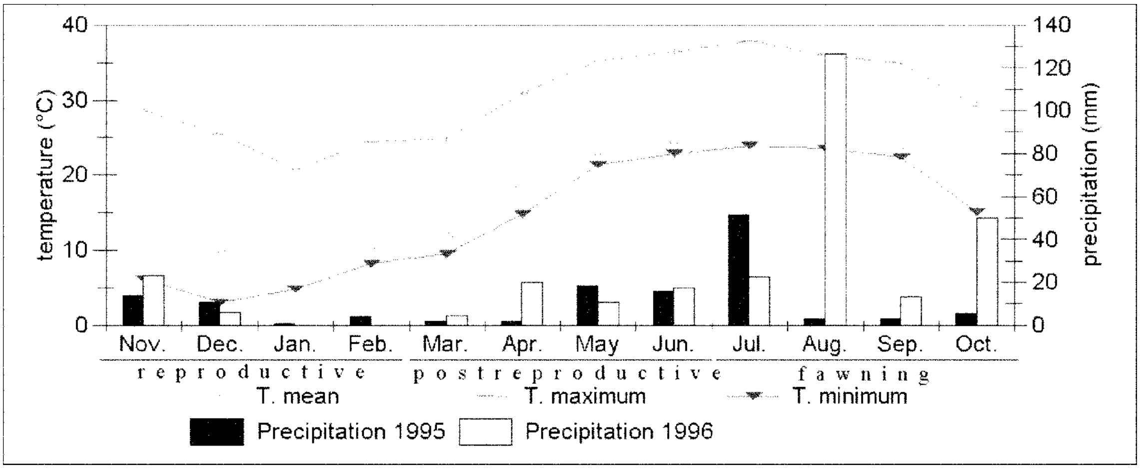

Fig. 2. Temperature and rainfall data during 1995 and 1996 for the Venustiano Carranza dam, localized 10 km from the study area.

The deer population varies from 80 to 100 animals. Vegetation in this zone is xerophyllous brushland that is found in a transitional zone between 2 physiographical provinces: the Coastal Plain of the Northern Gulf and the North American Great Plains (Briones 1984). The area has a variety of species characteristic of both provinces: cenizo (*Leucophyllum frutescens* Berl. Johnst), chaparro prieto (*Acacia rigidula* Benth), hojasen (*Flourensia cernua* DC), and gobernadora (*Larrea tridentata* (DC)Cov.). Briones (1984) determined 7 types of habitats for the municipality of Lampazos, Nuevo León, 6 of which were found in the study area: *Hilaria* grassland, *Leucophyllum* brushland, *Flourensia* brushland, *Acacia-Castela* brushland, *Prosopis* brushland, and *Acacia-Celtis* brushland. Additionally, after sampling the vegetation in this zone, we included another brushland habitat, *Opuntia*.

Vegetation Characteristics

Digital maps of vegetation and water sources on the San Francisco Ranch were made using the ILWIS geographic information system (ITC 1993). A map of habitats based on Briones's (1984) classification, was produced by aerial photograph interpretation (1:50,000), and field verification, which allowed us to correct the limits for some of the habitats.

Vegetal characteristics of each habitat type were estimated by first randomly establishing 400-meter-long transects, each with 10 sampling points in the 7 habitats. In all, 17 transects were established, and the number of transects per habitat varied from 1 to 9, depending on the relative area occupied by each habitat. The first point of a transect was placed randomly and the rest were spaced 40 meters apart. Brush species were sampled with the point-centered quarter method (Brower et al. 1990) at each point. For each point the following vegetation variables were measured: richness of plant species, height, distance from the nearest neighbor, density, horizontal and vertical vegetation cover. We also estimated volume of edible species, non-edible species, and total volume.

Thermal cover or protection offers shade which is important for ungulates exposed to heat stress (Mysterud and Ostbye 1999). We used the horizontal cover of brush (the horizontal area of plant foliage) as an estimate of thermal cover, and this was calculated by measuring 2 right angle diameters for each shrub and assuming the shape of an ellipse for the canopy.

Vertical cover was used as an indicator of hiding cover, which may benefit deer by reducing the possibility of detection and hence predation (Mysterud and Ostbye 1999). Hiding cover was estimated using a cover pole following the method described by Griffith and Youtie (1988). We used a 0.10 m x 2 m hardwood cover pole, with 4 horizontal divisions of 50 cm as strata labeled: 0–50 cm, 51–100 cm, 101–150 cm and 151–200 cm. Each stratum was painted with 5 alternating 0.1 m black and white bands. The cover pole was placed 15 m away from and perpendicular to each sampling point on the transect. From this position, 2 readings (1 on each side) were taken at each sampling point. Hiding cover estimates were calculated as the percentage of the pole concealed by vegetation at each stratum. Each painted band was equivalent to 20% cover. For these readings, a painted band was considered "covered" when at least 25% was obscured by vegetation. Average cover was obtained for each stratum as well as the total for each transect.

We calculated the total volume of each bush per transect assuming an approximated shape of an inverted cone. This value was used as an indicator of the biomass potentially available to deer. Although these values could be overestimated, especially for individuals of the *Opuntia* genus, we considered the bias would be constant among habitats. In addition, the volume of the most edibles species was determined as well as the volume of the less edible species. According to current literature (Martínez et al. 1997, Villarreal 1999), the 7 species important in the diet of deer are; *Acacia rigidula*, *A. berlandieri*, *A. greggi*, *Porlieria angustifolia*, *Prosopis* sp., *Opuntia* sp., and *O. leptocaulis*. We further determined the percentage of total volume of edible and less edible species for each habitat. We predicted the relative potential importance of each habitat for 3 basic requirements of deer (forage, thermal and hiding cover), in accordance with the values of habitat variables mentioned above.

We conducted a Principal Components Analysis (PCA) to order the vegetation transects relative to the selected habitat variables. This allowed us to determine which variables are associated with and characterize each of these habitats. The matrix was created using standardized and centered data which was then analyzed using the program STATISTICA (Statsoft 1998). Other variables also employed in this analysis were: variance in height, mean distance to the nearest neighbor, and variance in cover.

Radiotelemetry

From September 1994 through November 1995, we used a dropnet to capture 14 deer (7 males and 7 females). Each deer was equipped with a uniquely colored radiocollar with a specific frequency and activity sensor. Animals were relocated with a pair of TR-4 receptors (Telonics, Inc., Meza, Ariz.) and 2 portable "H"-type antennas at 2 fixed georeference stations. Paired compass readings per animal were taken simultaneously by hour over 24-hour cycles, with 2 or 3 cycles each month during 1995 and 1996. Although these data are autocorrelated, longer time intervals could produce larger variability within the data sets, reducing the comparison power and sacrificing behavioral information of biological significance (Reynolds and Laundré 1990). The Universal Transversal Mercator (UTM) coordinates were obtained using the Tripoly Program (Laundré 1990), assuming a magnetic deviation of 9.15°. For the purposes of sampling, we considered 3 deer biological periods, each with unique energy requirements: reproduction or breeding (November-February, the dry period), postreproduction or gestation (March–June, the dry period), and fawning (July–October, the rainy season).

Deer Habitat Preference

To analyze habitat preferences, we overlaid a vegetation map with the deer location coordinates, thus illustrating deer use for each habitat. A habitat was considered "preferred" when it was used to a greater extent than expected, according to its availability (Byers et al. 1984). Preference for each habitat was determined by 2 methods using the Generalized Linear Models program (GLIM; NAG 1993). We used GLIM because it is useful in handling difficult data sets (non-normal) and problems such as non-orthogonal designs (Crawley 1993). First, we regressed the seasonal number of locations of each individual within each habitat against the area of each habitat. This enabled us to test if the number of locations by habitat type depended on its availability, and on the variables sex, season, or year. A positive regression indicated that the number of locations was determined by the availability of each habitat, while any other result indicated preferences for certain habitats. Second, a log-linear model assuming a Poisson error distribution was used to determine which habitats were either preferred or avoided, and whether preferences were affected by the variables: habitat (6 levels), sex (2 levels), season (3 levels), and year (2 levels). We use the log-linear model because it allows us to detect changes in preferences related to factors such as individual (sex, age) and time as year and season (Manly et al. 1993). When we fitted the models of preferences analysis, there was overdispersion of the scale factor, which could have produced an error in the test of hypothesis. Therefore, we calculated the scale factor from the residual deviance before running the analysis with overdispersion, and used the F statistic distribution as reference (Crawley 1993).

Deer Activity

We recorded the behavior of deer at the same time the animals were relocated. The type of behavior was identified by counting the number of beeps emitted by the activity sensor per minute during 5 min intervals. In an earlier study with captive deer using collars with sensors, Mandujano et al. (1996) demonstrated 90% accuracy in distinguishing 3 activity patterns of the deer behavior based on the beep frequency: bedding (50–55 beeps per minute), searching (56–69 beeps per minute) and feeding (70–87 beeps per minute). We counted the number of locations per habitat classified by activity (bedding, searching, and feeding) by sex, season and year. The number of locations expected for each activity in each habitat was calculated by multiplying the total number of locations by activity by the relative availability of each habitat. We determined habitat preferences by activity using a chi-square analysis in GLIM. When there were problems of overdispersion in the models, these were dealt with by using a correction factor similar to that used in the preference analyses.

Results

Vegetation Characteristics

Based on the attributes of the 7 habitats (Table 1), we ranked the different habitats relative to their importance value for deer requirements as follows.

Table 1. Variables in each habitat type on the San Francisco Ranch, Mexico and their relative potential importance for 3 basic requirements of deer. (A = *Acacia-Castela*, F = *Flourensia*, H = *Hilaria*, L = *Leucophyllum*, O = *Opuntia*, P = *Prosopis* and C = *Acacia-Celtis*; for importance value 1 = low, 2 = medium, and 3 = high).

	Habitat						
Variable	A	F	H	L	O	P	C
Transect number	9	2	1	1	1	2	1
Richness (No. species)	10	11	9	10	5	7	6
Brush density (ind/ha)	199	265	5	118	10	49	81
Thermal cover (m^2)	62.7	49.7	53.6	45.4	51.9	88.6	154.6
Hiding cover 0–50(%)	60.2	56.0	15.0	68.0	8.3	76.0	100.0
Hiding cover 51–100(%)	39.1	13.5	2.0	25.0	0.0	54.5	95.0
Total hiding cover(%)	39.5	25.0	6.3	34.3	2.8	52.5	97.0
Mean distance (m)	3.6	2.8	21.4	2.9	10.2	4.5	3.5
Mean height (m)	1.2	1.0	1.5	1.2	0.8	1.4	2.4
Variance thermal cover (m^2)	2.8	2.4	1.4	1.0	2.8	4.6	14.8
Variance height (m)	0.2	0.1	6.8	0.1	0.1	0.2	0.9
Total volume (m^3)	37.5	29.6	37.7	26.7	16.8	58.3	187.1
Edible Species volume (m^3)	13.7	14.5	28.5	7.6	16.3	39.6	127.4
Not edible Species volume (m^3)	23.7	15.1	9.2	19.2	0.5	18.6	59.7
Edible volume percentage (%)	41.2	35.8	75.5	28.4	96.9	64.7	68.1
Not edible volume percentage (%)	58.8	64.2	24.5	71.6	3.1	35.3	31.9
Foraging value	1	1	2	1	1	3	3
Hiding value	3	2	1	2	1	3	3
Thermal value	3	2	1	1	1	3	3

Table 2. Results of Principal Components Analysis of habitat variables for component 1 and component 2 on the San Francisco Ranch, Mexico (*= P < 0.05).

Variable number	Variable	Component 1	Component 2
1	variance thermal cover (m^2)	–0.589	–0.434
2	variance height (m)	–0.925 *	–0.128
3	Brush density(ind/km^2)	0.314	0.664
4	Richness (No. Species)	0.323	0.209
5	Thermal cover (m^2)	–0.932*	–0.162
6	Hiding cover 0–50 (%)	–0.646	0.683
7	Hiding cover 51–100 (%)	–0.759*	0.517
8	Total hiding cover (%)	–0.799*	0.519
9	mean distance (m)	0.098	–0.891*
10	mean height (m)	–0.905*	–0.281
11	total volume (m^3)	–0.970*	–0.136
12	Edible Species volume (m^3)	–0.887*	–0.293
13	Not edible Species volume (m^3)	–0.824*	0.207
14	Edible volume percentage (%)	–0.090	–0.676

Forage: Although *Acacia-Celtis* brushland was comprised of only 6 species, including small trees of *Acacia farnesiana*, this habitat had the highest total and edible species volume, and was considered to provide good conditions for foraging activity. Mean height was 2.6 m and this habitat was common around the ephemeral streams and their dams. Although vegetation density was low, we considered *Prosopis* brushland a good foraging habitat because it had the second highest volume of edible species, and a richness of 7 species. In the *Hilaria* habitat we included some man-made meadows mixed with fragments of other habitats found at the study area. Nine plant species were detected. Although this habitat had the lowest individual density, its bushes were relatively tall (mean height 1.5 m) and 75% of total volume was edible, thus this habitat could be an important source of forage for deer. The *Acacia-Castela* brushland had 10 species and a mean brush density of 199 individuals/ha, however the volume of edible species was one of the lowest and we considered it less important for deer foraging. We considered *Flourensia*, *Leucophyllum* and *Opuntia* to be unattractive habitats for foraging because they had a low volume of edible species, even though *Flourensia* and *Leucophyllum* had high species richness. We did however find a few signs of browsing on *Opuntia* by deer on the ranch.

Hiding cover: With the highest values of overall hiding cover. *Acacia-Celtis*, *Prosopis* and *Acacia-Castela* provided good conditions for bedding and searching. The *Leucophyllum* brushland had high hiding cover in the 0–50 stratum, and although it diminished in the other 2 levels, we still considered it as good protection habitat by deer. In the case of *Flourensia* brushland, the hiding cover in the 0–50 stratum, important for fawns, was 56%, but total cover was among the lowest because mean height was only 1.0 m. Finally, the *Hilaria* and *Opuntia* habitats had the lowest values for hiding cover, and were considered the least important for deer protection against predators.

Thermal cover: *Acacia-Celtis*, *Prosopis* and *Acacia-Castela* habitats had the highest thermal cover and offered good conditions as bed sites of deer. *Flourensia* brushland had the highest density of individual plants, but lower thermal cover compared to the above habitats. Thermal protection diminished in *Hilaria*, *Opuntia* and *Leucophyllum* (the lowest) habitats and we considered these habitats as unattractive as bedding sites.

The transect ordination shown in Figure 3a is based on the first 2 principal components, which accounted for 74% of the variance. The first component (51% variance explained) was correlated significantly with total volume, volume of edible and non-edible species, thermal and hiding cover, and variance in cover (Table 2). This component effectively separated habitats relative to cover and food: *Acacia-Celtis* and *Prosopis*, as well as 2 *Acacia-Castela* transects that registered the highest values of the abovementioned variables for this habitat vs the habitats of *Leucophyllum*, *Flourensia*, *Hilaria*, and *Opuntia* with lower cover and volume (Fig 3a and 3b). The second component (23% of the variance explained) separated the dense habitats from the open ones, as indicated by the mean distance between individual plants. The *Opuntia* and *Hilaria* habitats were the most open habitats with average distances of 21.3 and 10.2 m, respectively.

Habitat Preferences By Deer

We recorded 4,909 deer locations and these varied per sample populations from none in the *Opuntia* habitat to 926 in *Acacia-Castela* brushland (Table 3). As deer did not use the *Opuntia* habitat, we did not include it in the GLIM analysis, and thus avoided bias in the preferences

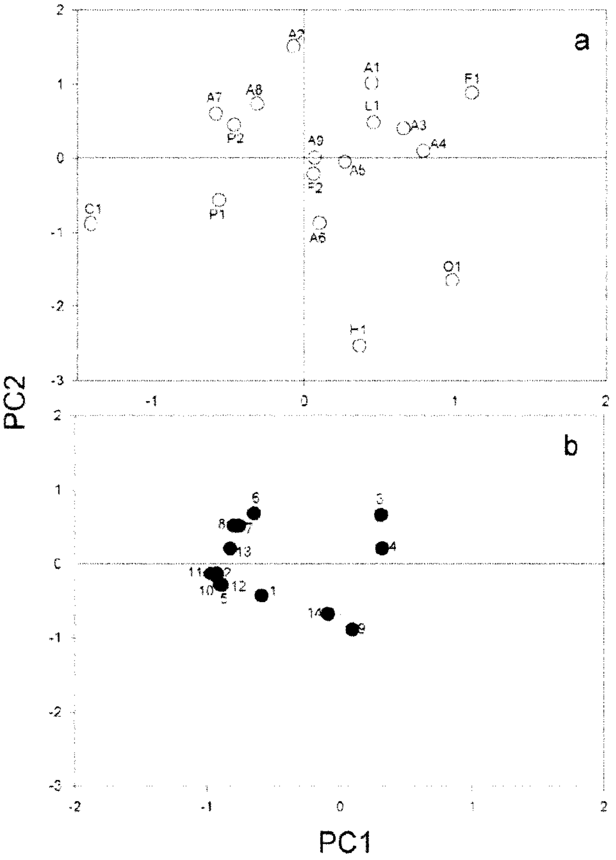

Fig. 3. Principal Components Analysis for vegetation transects on the San Francisco Ranch, Mexico(a) and relationship among environmental variables of the Table 2 (b). (A = *Acacia-Castela*, F = *Flourensia*, L = *Leucophyllum*, H = *Hilaria*, O = *Opuntia*, P = *Prosopis* and C = *Acacia-Celtis*).

Table 3. Estimated area, and location numbers of white-tailed deer for each habitat association by sex on the San Franscisco Ranch during 1995 and 1996. Percentages are shown in brackets.

		1995		1996	
Plant association	area (ha)	female	male	female	male
Opuntia	11 (1.1)	0	0	0	0
Hilaria	30 (3)	15 (1)	42 (3)	82 (6)	89 (10)
Leucophyllum	117 (11.6)	13 (1)	115 (9)	178 (13)	251 (29)
Flourensia	60 (5.9)	212 (15)	243 (18)	127 (10)	19 (8)
Acacia-Castela	546 (54)	926 (65)	658 (51)	673 (51)	316 (49)
Prosopis	149 (14.7)	76 (5)	89 (7)	61 (5)	23 (8)
Acacia-Celtis	98 (9.7)	191 (13)	146 (11)	195 (15)	169 (11)

analysis by small frequencies. We found a positive relationship (r = 0.55, P < 0.05) between habitat availability and the number of locations by habitat (Fig. 4a), but the data formed 2 separate clusters that correspond to the *Acacia-Castela* brushland and the other 5 habitat types. Suspecting that the high availability of *Acacia-Castela* brushland (54%) was responsible for this result, we performed a second regression analysis (Fig. 4b) excluding this habitat type. The result was no relationship between habitat availability and frequency of locations (r = 0.06, P > 0.05). The lack of correlation between these 2 variables indicates habitat preference on the part of deer, and the preference was masked by the high availability of *Acacia-Castela* brushland.

Preferences were influenced by habitat type, sex, and year ($F_{5,156}$ = 13.5, *P*<< 0.00001). During 1995, females avoided *Hilaria* and *Leucophyllum,* while they preferred areas of *Flourensia*, *Acacia-Castela*, and *Acacia-Celtis*. The high cover *Prosopis* habitats were used according to availability (Fig. 5a). Males however, selected most of the habitat types according to availability, showing preference only for *Flourensia* habitats. During 1996, females preferred *Hilaria,* avoided *Prosopis* and *Acacia-Castela* habitats, while their use of *Leucophyllum, Flourensia,* and *Acacia-Celtis* was based on relative availability (Fig. 5b). Males preferred *Hilaria* and *Acacia-Celtis* habi-

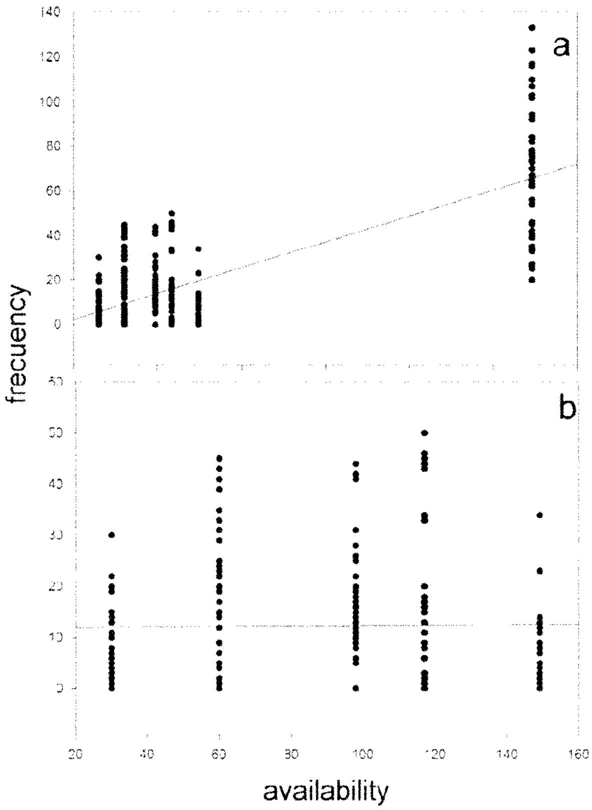

Fig. 4. Regression analysis of data on habitat use of deer and availability of each vegetation association on the San Francisco Ranch, Mexico with (a) and without (b) the *Acacia-Castela* habitat.

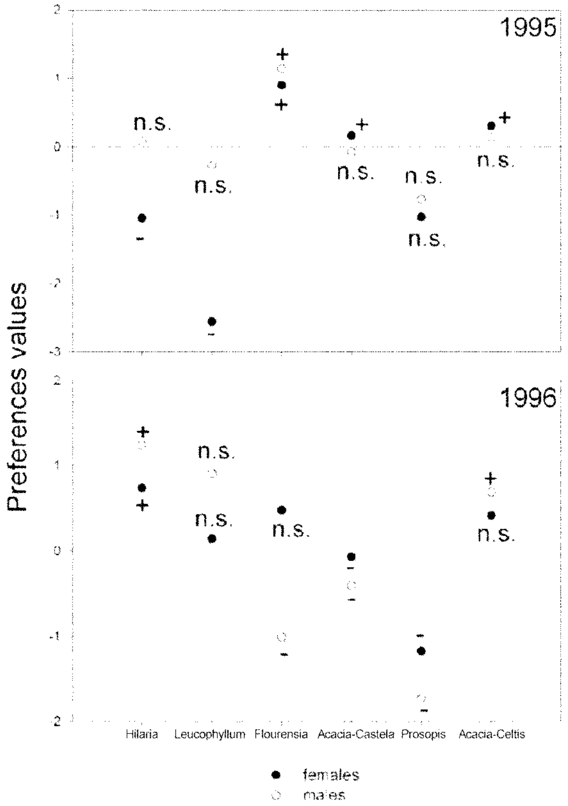

Fig. 5. Habitat preferences of white tailed deer by sex on the San Francisco Ranch, Mexico during 1995 (a) and 1996 (b). The sign "+" indicates preference, the sign "–" indicates avoidance, "n.s" indicates use according to availability.

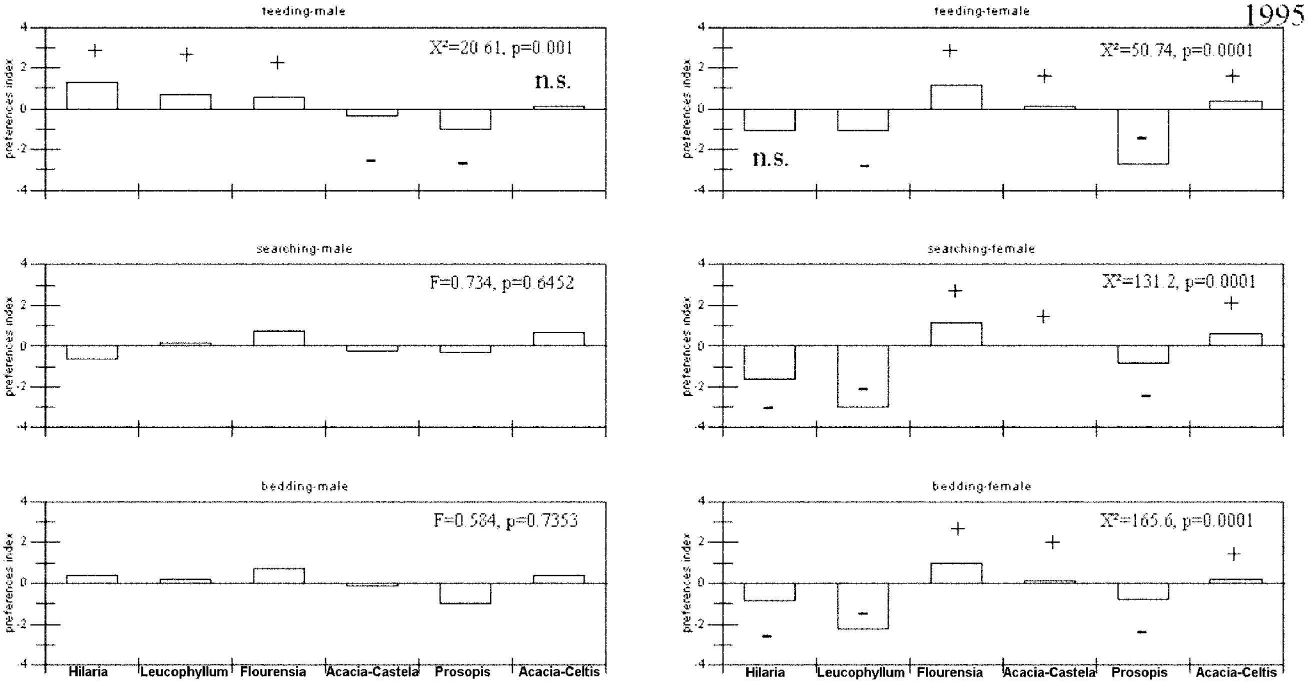

Fig. 6. Deer activity in each habitat by sex in 1995 on the San Francisco Ranch, Mexico. The sign "+" indicates preference, the sign "–" indicates avoidance, "n.s" indicates use according to availability.

tats, while *Flourensia*, *Acacia-Castela*, and *Prosopis* were avoided (Fig. 5b).

Deer Activity

There was also variation in each habitat for the 3 activities studied between sexes and years (Fig. 6). Both sexes used the *Prosopis* brushland less than expected, for the 3 activities during both years. For feeding activity during 1995, males preferred the *Hilaria*, *Leucophyllum* and *Flourensia* habitats and avoided *Acacia-Castela* and *Prosopis*. Females preferred the *Flourensia*, *Acacia-Castela* and *Acacia-Celtis* habitats for all activities and avoided *Hilaria*, *Leucophyllum* and *Prosopis*. In 1996, males preferred *Hilaria*, *Leucophyllum* and *Acacia-Celtis* for all activities (Fig. 7). They avoided *Flourensia*, for feeding and bedding and *Acacia-Castela* and *Prosopis*, for all 3 activities. In 1996, females used all the habitats according to availability for all 3 activities. *Hilaria* was used more by females than in 1995, and there was less use of *Flourensia* and *Acacia-Celtis* than in 1995.

Discussion

The habitats found within the San Francisco Ranch had markedly different characteristics, some had high cover values and others a high value of edible species. Therefore each habitat can, depending on its specific environmental conditions, meet different requirements for deer. Accordingly, we found that deer did exhibit habitat preferences and that these preferences for different habitats depended on sex and year. Habitats with dense cover, with the exception of *Prosopis*, were important for all female activities during 1995, whereas males only preferred the dense cover zones of *Acacia-Celtis* in 1996. Cover protection against predators and harsh temperatures is an important element in deer habitat (Kroll 1992, Olson 1992). In Texas, the areas most heavily used by deer have dense cover that often exceeds 80% (Pollock et al. 1994); on the San Francisco Ranch, *Acacia-Castela*, *Prosopis* and *Acacia-Celtis* brushland also had hiding cover with similar values. Wiggers and Beasom (1986) state that in general, cover of 53% or more is considered favorable to white-tailed deer, because it offers protection against predators such as coyote (*Canis latrans*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*). It has been determined that on the San Francisco Ranch, deer make up 8% of the coyote's diet (López-Rivera and Gallina 1998). Predation data for cougars is limited and unavailable for the bobcat. Although these predators are found in our study area, and the fences did not limit their movements in and out of the ranch, predation was generally low. The main difference between years is a result of more deer being attacked and killed in 1995 when, perhaps attracted by the abundant drinking water, 2 dogs entered the study area. DeStefano et al. (2000) address the issue of water developments attracting predators and impacting prey populations. According to workers on this ranch, there were more deaths in 1995 than in 1996. These dogs were killed at the end of the fawning period in 1995 and were not a problem in 1996, although cougars and coyotes continued to be present. This was the only measure of predator control taken during the study period. The drought conditions that influenced the physical condition of the deer during 1995, as well as predation by the feral dogs, could have caused the deer to adopt a defensive strategy. This may explain why females preferred locations with good cover, such as the *Acacia-Castela* and *Acacia-Celtis* plant associations during 1995.

In general, males showed limited habitat preference in 1995, and during 1996 they preferred open areas, only using certain habitats of dense cover. Therefore, they depended on dense cover zones for fewer activities than females did. This preference for open habitats contrasts with results from other studies (Wood et al.

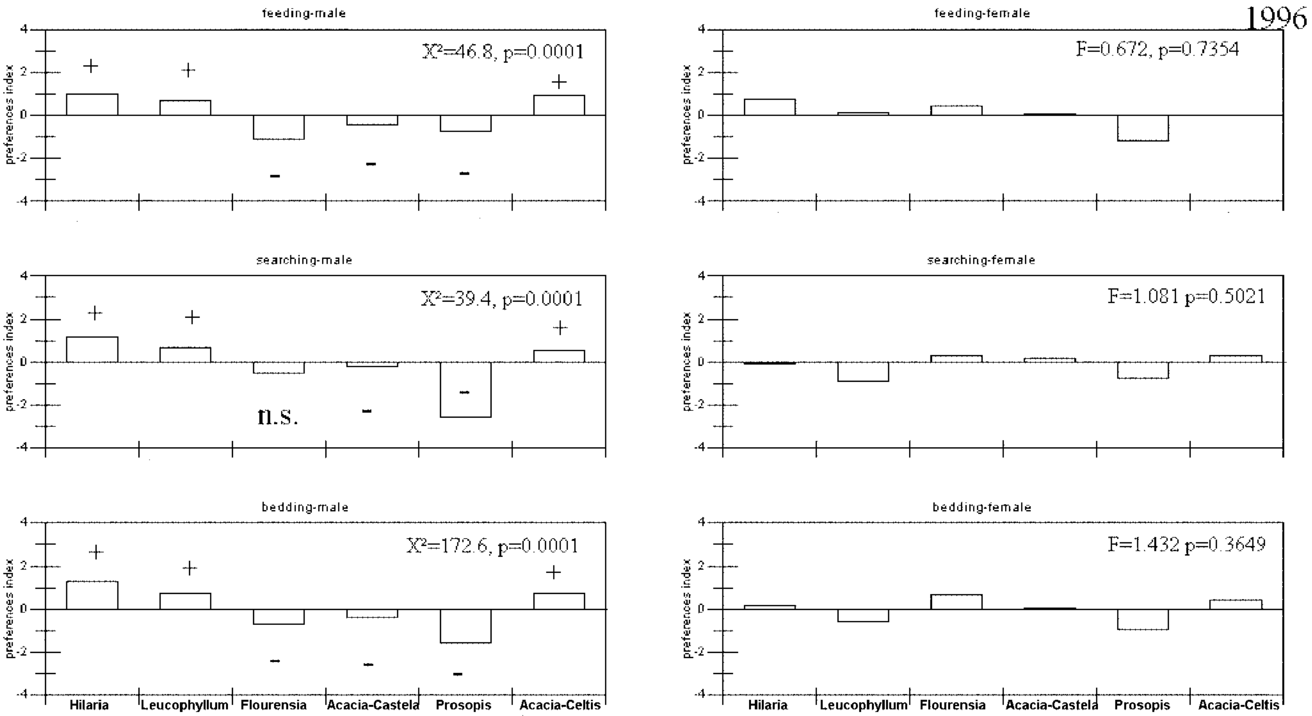

Fig. 7. Deer activity in each habitat by sex in 1996 on the San Francisco Ranch, Mexico. The sign "+" indicates preference, the sign "-" indicates avoidance, "n.s" indicates use according to availability.

1989, Ockenfels et al. 1991) which show that deer of both sexes tend to avoid open areas. In fact, there are areas where cover is thought to be the determining factor in selection, more for favorable thermal cover conditions than hiding cover (Bowyer et al. 1998). This selection is a result of frequent high temperatures (over 30°C) that cause water loss from evapotranspiration (Ockenfels and Bissonette 1984). Under these harsh circumstances, deer move to areas with good cover in order to avoid thermal stress (Pollock et al. 1994). The different male behavior observed on the San Francisco Ranch could be due, as we expected, to the high availability of water, but also to the good vegetation cover, which allowed them to venture beyond dense cover zones to open areas such as *Hilaria* and *Leucophyllum* to forage and search. This behavior has been reported in other studies (Mysterud and Ostbye 1999)

Females preferred zones with high cover during 1995, but not in 1996. Both the habitats they avoided and those that they preferred during 1995, were used according to habitat availability in 1996. This variation is probably a result of the marked differences in precipitation between years (1995: 136 mm; 1996: 276 mm). Because drinking water was abundant in both years owing to the water management program, the yearly variation in habitat use was likely a result of some other changes in habitat characteristics that we did not measure. Since we only have data for 2 years, it is difficult to analyze this possibility with any greater precision. Nevertheless, variability in precipitation in arid zones has been observed to modify habitat conditions (Davis 1990), mainly the availability of food and cover (Kie and Thomas 1988). Seasonal variation in site use as a result of these sources of variation, as well as individual requirements, has been reported in other studies (Orians and Wittenberger 1991, Pollock et al. 1994). Thus the higher precipitation in 1996 likely improved forage conditions in all the habitats of the San Francisco Ranch, and gave deer a greater selection from which to choose. This resulted in greater use of open areas by females in 1996 compared to 1995, and could explain why females used *Acacia-Celtis* less for feeding during 1996.

Females avoided *Hilaria* habitat during 1995, but preferred it in 1996. When we look at the habitat preferences by activity, the use of *Hilaria* for feeding activity increased during this wet year, likely because it had a greater diversity of nutritious, edible species according to Davis (1990). This association is comprised of a mixture of grassland and dense brushland; such a combination is attractive for deer (Wood et al. 1989, Kroll 1992) as it encourages the production of herbaceous species and greater diversity of brush species, both important elements in deer diet during the rainy season (Rollins et al. 1988). *Flourensia* was important for the feeding activity of both sexes in 1995, and for males in 1996. *Leucophyllum* was preferred by males during 1996. Both of these plant habitats had less food available than the other types and, in particular, *F. cernua* is not very palatable browse (Estell et al. 1994). The use of these 2 habitats could be explained by their relatively high species richness, which provided a variety of plants and plant parts that allow deer to meet their dietary needs (Davis 1990). The few signs of browsing on *Opuntia* by deer we observed on the ranch, may indicate that deer consume *Opuntia* to complement nutrient intake, but this is a subject for further study.

Conclusions

The behavior of white-tailed deer on the San Francisco Ranch differs markedly from that observed in arid zones where water is a limiting factor. Thermal cover requirements for protection against extreme temperatures were relatively low during 1996 as precipitation that year was higher than in 1995. In general, this improved habitat conditions and, specifically, increased thermal and hiding cover, food availability and reduced thermal stress. This may explain why open zones were preferred while the *Prosopis* zone, with high hiding and thermal cover, was avoided. The need for hiding cover decreased in 1996 since predation by dogs was eliminated. In contrast, 1995 was characterized by extreme drought and, although drinking water was abundant, food availability was lower. Deer sought and used dense cover more frequently, and were subjected to higher predation, mainly by dogs. The observed variation in the preferences of both sexes from year to year reminds us that habitat use is a complex process. For arid zones during years when drinking water is available all year round, and when predation is low and weather conditions are good with normal to abundant precipitation, the quality (i.e. diversity of species) and quantity of available forage is a key factor in determining habitat use by deer. However, when drought or predation increases, thermal and hiding cover become relatively more important than forage availability. From this we can conclude that, in addition to the availability of drinking water, effective water management programs in arid zones must also consider taking measures to maintain brushland with good thermal and hiding cover for deer to mitigate the effects of harsh weather and predation.

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Grassland birds associated with agricultural riparian practices in southwestern Wisconsin

ROSALIND B. RENFREW AND CHRISTINE A. RIBIC

Authors are graduate student and unit leader/associate professor, USGS BRD Wisconsin Cooperative Wildlife Research Unit, Department of Wildlife Ecology, 1630 Linden Drive, University of Wisconsin, Madison, Wisc. 53706.

Abstract

Rotational grazing has been proposed as a Best Management Practice (BMP) for minimizing runoff in Wisconsin agricultural riparian areas. The influence of this land management practice on grassland birds has not been evaluated in relation to more traditional agricultural land management systems in Midwestern riparian areas. This study compared the grassland bird community in riparian areas in Wisconsin that were rotationally grazed to 2 common land use practices along streams in Wisconsin: continuously grazed pastures and rowcrop fields with 10-m-wide ungrazed buffer strips located along the stream. We calculated total number of birds, the Berger-Parker Index of Dominance, and number of birds ha^{-1} for each site. Vegetation variables used were height-density, litter depth, and percent bare ground. Bird species richness, species dominance, and density did not differ among land use types. In contrast, grassland bird species of management concern [Savannah Sparrow (*Passerculus sandwichensis* Gmelin), Eastern Meadowlark (*Sturnella magna* L.), and Bobolink (*Dolichonyx oryzivorus* L.)] were found on continuous and rotational pastures but very rarely or never occurred on buffer strips. Contrary to previous research, however, rotationally grazed pastures did not support more of these species than continuously grazed pastures. Bird density was related to vegetation structure, with higher densities found on sites with deeper litter. Within the pasture land use types, there were no consistent differences between species richness and density near the stream (<10 m) and away (>10 m).

Key Words: pastures, rotational grazing, species richness, density, dominance, buffer strips

Resumen

El apacentamiento rotacional ha sido propuesto como una Buena Practica de Manejo (BPM) para minimizar el escurrimiento en las áreas ribereñas agrícolas de Wisconsin. La influencia de esta practica de manejo de tierras en las aves del pastizal no ha sido evaluada en relación a los sistemas mas tradicionales de manejode las áreas ribereñas del medio oeste. Este estudio comparó la comunidad de aves de pastizal en áreas ribereñas apacentadas rotacionalmente contra dos prácticas comunes utilizadas a lo largo de corrientes de agua en Wisconsin: potreros apacentados continuamente y campos sembrados con cultivos en surcos y con franjas de amortiguamiento sin apacentar de 10 m de ancho localizadas a lo largo de las corrientes. Calculamos el número de aves, el indice de dominancia ed Berger-Parker y el número de aves ha^{-1} para cada sitio. Las variables de vegetación utilizadas fueron: altura-densidad, profundidad del mantillo y porcentaje de suelo desnudo. La riqueza de especies de aves, dominancia de especies y densidad no difirieron entre los tipos de uso de la tierra. En contraste, las especies de aves del pastizal de interés de manejo, [Savannah Sparrow (*Passerculus sandwichensis* Gmelin), Eastern Meadowlark (*Sturnella magna* L. and Bobolink (*Dolichonyx oryzivorus* L.)] se encontraron en los potreros apacentados rotacional y continuamente, pero muy raramente o nunca se encontraron en las franjas de amortiguamiento. Sin embargo, Contrario a la investigación previa, los potreros apacentados rotacionalmente no sostienen mas de estas especies que lo que sostienen los potreros apacentados continuamente. La densidad de aves se relaciono a la estructura de la vegetación, con mayores densidades encontradas en sitios con mantillo profundo. Dentro de los tipos de uso de los potreros no hubo diferencias consistentes entre la riqueza de especies y la densidad cerca de las corrientes (< 10 m) o lejos de ella (> 10 m).

Grassland birds have been declining faster and more consistently than any other avian guild in North America in the last 30 years (Knopf 1995). Pastures in Wisconsin support several breeding grassland bird species of management concern (Sample and Mossman 1997, Wisc. Natural Heritage Program 1999), including Grasshopper Sparrow (*Ammodramus savannarum* Gmelin), Eastern Meadowlark (*Sturnella magna* L.), Western Meadowlark (*Sturnella neglecta* Audubon), Bobolink (*Dolichonyx oryzivorus* L.), Sedge Wren (*Cistothorus platensis* Latham), Upland Sandpiper (*Bartramia longicauda* Bechstein), and Savannah Sparrow (*Passerculus sandwichensis* Gmelin). Management of grasslands for the benefit of these species is a priority in Wisconsin and elsewhere (e.g., Jones and Vickery 1996, Swanson 1996, Herkert 1991, Herkert et al. 1996).

The purpose of this study was to compare the avian communities of management intensive rotationally grazed (MIRG) riparian areas to those in 2 common riparian land management options in southwestern Wisconsin: continuously grazed (i.e., conventional)

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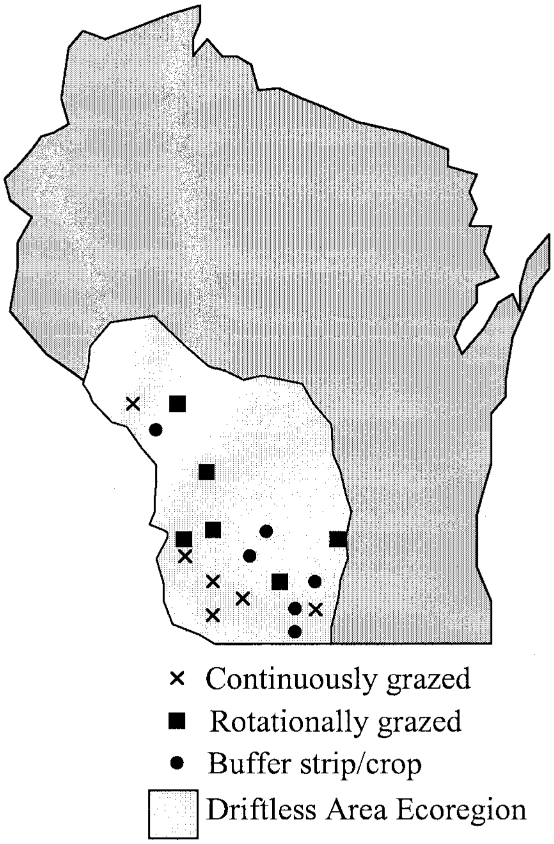

Fig. 1. Location of study sites in southwestern Wisconsin.

riparian pastures and row crops with 10-m-wide ungrazed grassy buffer strips along streams (buffer strip/crops). In addition, within the 2 pasture management types, we compared the avian communities near the stream (<10 m) and away from the stream (>10 m) to evaluate the within-pasture distribution of birds.

Materials and Methods

Study area and sites

Study sites were located along cold-water streams and distributed throughout the Driftless Area in southwestern Wisconsin (Lat. 43° 00', Long. 90° 22') (Fig. 1). Sites were chosen as part of an interdisciplinary study to assess the impacts of rotational grazing on riparian streams.

Each land use type (continuous grazing, rotational grazing, and buffer strip/crops) was replicated on 4 riparian sites in 1996, but only 2 of the 4 sites from each type were revisited in both 1997 and 1998 because land use changes disqualified some sites each year. These disqualified sites were replaced with new sites to maintain a total of 12 sites (four sites per land use type) each year. All sites had been under a particular land use for at least 3 years.

Average sizes of continuous and rotational pasture sites were 12.1 ha (range = 5.1-17.9 ha) and 12.4 ha (range = 2.5–35.5 ha), respectively, with the stream generally running through the middle of the pastures. Pastures were dominated by sedges (*Carex* spp.) and Kentucky bluegrass (*Poa pratensis* L.) near and away from streams, as well as white clover (*Trifolium repens* L.) and quack-grass (*Elytrigia repens* L.) away from streams. Grassy buffer strips were approximately 10-m wide on each side of the stream and were surrounded by cornfields. Buffer strips averaged 410 m in length (range = 200–450 m) and were steeply sloped within 5 m of the stream. Reed canary grass (*Phalaris arundinacea* L.) and sedges were the dominant plant species in buffer strips, and 0 to 8 shrub plants were interspersed along the buffers at each site. Streams were 1 to 2-m wide and 0.2 to 1-m deep.

Bird surveys

Birds were surveyed using standard 50-m-radius, 5-min point counts (Ralph et al. 1997). Three point count surveys were conducted at each site from mid-May to the end of June, with approximately 2 weeks between each survey. The number of points varied among sites based on site size (range = 1–5). Points were centered over streams and were separated by at least 150 m to avoid double counting birds. Points were located so as to fit as many points as possible that contained no trees or fences and were at least 25 m from pasture and row crop edges when possible. If only 1 point fit into a pasture, it was located as close as possible to the center of the site. In pasture sites, birds located within 10 m of the stream were recorded separately from all other birds to compare bird communities near (<10 m) versus away (>10 m) from streams. The amount of stream area and non-stream area surveyed was calculated for each point circle using distances estimated by pacing the stream length or by calculating areas with a planimeter on aerial photos.

Vegetation structure

Each year of the study, vegetation data were collected from each study site during the last week in April or the first week in May when breeding birds are establishing territories. Sampling design was a stratified random pattern involving 3 transects perpendicular to the stream on each side of the stream, for a total of 6 transects per site. Three sampling locations along each transect provided a total of 18 observations for each site on each date. Along each transect, 1 sample was collected within 3 m of the stream. The other 2 samples were collected at randomly chosen stations at least 10 m away from the stream (upland) along each transect by taking a random number of steps away from the previous location. Data from the 2 upland locations were averaged for analyses. At each sampling location, a 0.5 m^2 Daubenmire frame (Daubenmire 1968) was used to obtain estimates of percent bare ground, percent litter cover, percent live vegetation cover, and percent of live cover that was grass, legume or forb. Four random litter depth (cm) measurements were taken within each Daubenmire frame and the results averaged for that sampling location. A Robel pole was used in the center of the frame to obtain vegetation height-density (cm) (visual obstruction measurements) and maximum vegetation height (cm). The procedure used was modified from the original Robel method (Robel et al. 1970) by reading the pole from a single height of 1.5 m rather than from 3 different heights. Readings were taken from the 4 cardinal directions and averaged for each location.

Data Analysis

Bird species present at a site for 1 or more years were treated as occurring on that site. Species were tabulated by land use type and near/away from the stream. Species were categorized as to their general habitat preferences (i.e., forest, wooded edge, grassland/ cropland, riparian, urban/farmstead, and wetland) (Best et al. 1996). Bird densities (birds ha^{-1}) for each site were averaged over the 3 surveys. Bird densities near and away from the stream and densities of only the grassland birds were similarly calculated. Species richness for each site was calculated by counting the number of species seen for all 3 surveys within a year. Species richness near and away from the stream were calculated similarly. Community metrics of species richness, dominance, and overall similarity were calculated for each land use type within each year. The Berger-Parker Index of Dominance (max [number of individuals of species *i*]/total number of individuals seen) (Magurran 1988) was calculated for each survey on the site and then averaged for a dominance index for each site. The larger the number, the more numerically dominant a single species was in the community. Dominance indices for near and away from stream were similarly calculated.

Due to changes in some sites from between years, analyses were performed for each year separately. Differences in average site species richness, dominance, density, and average similarity among land use types were tested using generalized linear models (McCullagh and Nelder 1989). Species richness and the Dominance Index were adjusted for effort (Magurran 1988) by including area surveyed as the first term in the models (e.g., when testing for the effect of land use type, the model would be index = overall mean + area surveyed + land use type + error). To evaluate differences between the pasture land use types in the indices between areas near and away from streams, we paired on site (i.e., “near” and “away” were paired) for a split-plot analysis of variance. When an interaction between land use types and near/away status occurred, paired t-tests were used to assess differences in species richness, dominance, or density within each pasture land use type.

Percent bare ground, litter depth, and vegetation height-density were used to assess the importance of vegetation structure in explaining the variation in the bird community metrics. For these analyses, values for each vegetation variable was averaged over the entire site. Species richness and total density for the land use types were modeled with the vegetation variables using backward stepwise generalized linear models (McCullagh and Nelder 1989). Generalized linear models with a Poisson and gaussian error structure were used for species richness and density analyses, respectively. Differences in the community metrics and vegetation for near/away from streams in the pastures were also analyzed using generalized linear models with a gaussian error structure. Individual species distributions within a pasture were not analyzed due to low sample sizes. Trends were assessed at an alpha of 0.10 and significance at 0.05. All analyses were performed using Splus 4.5 (Mathsoft 1998).

Results

Bird community comparison among land use types

Twenty-five bird species were recorded over the 3 years (Table 1); 40% of these species are considered to be associated with

Table 1. Complete species list for near (<10 m) and away (>10 m) from stream in the 3 land use options.

		Treatments					
		Continuous		Rotational		Buffer strip/Crop	
Species	Habitat	near	away	near	away	near	away
Great Blue Heron (*Ardea herodius*)	W[1]	X					
Wood Duck (*Aix sponsa*)	W	X					
Mallard (*Anas platyrhynchos*)	W	X		X		X	
Killdeer (*Charadrius vociferus*)	G	X	X		X		
Spotted Sandpiper (*Actitis macularia*)	W					X	
Common Snipe (*Gallinago gallinago*)	W	X					
Belted Kingfisher (*Ceryle alcyon*)	R	X	X			X	
Willow Flycatcher (*Empidonax traillii*)	E					X	
Eastern Phoebe (*Sayornis phoebe*)	R			X	X		
Eastern Kingbird (*Tyrannus tyrannus*)	E		X	X	X		
Blue jay (*Cyanocitta cristata*)	F		X				
Sedge Wren (*Cistothorus platensis*)[2]	G	X	X				
Eastern Bluebird (*Sialia sialus*)	E	X			X		
American Robin (*Turdus migratorius*)	E	X	X	X	X		X
European Starling (*Sturnis vulgaris*)	U		X				
Common Yellowthroat (*Geothylypis trichas*)	E				X	X	
Chipping Sparrow (*Spizella passerina*)	E		X				
Savannah Sparrow (*Passerculus sandwichensis*)[2]	G	X	X	X	X	X	
Song Sparrow (*Melospiza melodia*)	E	X	X	X	X	X	X
Bobolink (*Dolichonyx oryzivorus*)[2]	G		X		X		
Red-wing Blackbird (*Agelaius phoeniceus*)	W	X	X	X	X	X	X
Eastern Meadowlark (*Sturnella neglecta*)[2]	G		X		X		
Common Grackle (*Quiscalus quiscula*)	E		X				
Brown-headed Cowbird (*Molothrus ater*)	E	X	X	X	X		
American Goldfinch (*Carduelis tristas*)	E		X	X	X	X	
Total Species		13	16	9	12	9	4

[1] Habitat with which species is associated. E = Wooded edge (forest edge, shrubland, oldfield); F = Forest; G = Grassland/Cropland; R = Riparian (usually wooded); U = Urban/farmstead; W = Wetland (Best et al. 1996).

[2] Grassland bird species of management concern.

Table 2. Bird community parameters for each year (n = 4).

Species Land Use Type	Richness	Dominance[1]	Density	Species of Management Concern Density	Species of Management Concern Number
	-(No. site^{-1})-		-(No. ha^{-1})-	-(No. ha^{-1})-	
1996					
Continuous[2]	5.5 ± 2.13	0.50 ± 0.17	2.35 ± 0.83	1.96 ± 0.79	3
Rotational	4.3 ± 0.5	0.42 ± 0.06	1.89 ± 0.57	1.27 ± 0.17	2
Buffer strip/crop	3.3 ± 0.5	0.34 ± 0.12	3.52 ± 0.90	0.21 ± 0.21	1
1997					
Continuous	5.3 ± 1.3	0.39 ± 0.60	3.31 ± 1.18	4.69 ± 1.87	3
Rotational	3.0 ± 0.9	0.62 ± 0.15	2.78 ± 0.88	3.18 ± 1.35	1
Buffer strip/crop	3.5 ± 0.5	0.54 ± 0.05	4.56 ± 1.06	0	0
1998					
Continuous	3.5 ± 1.2	0.56 ± 0.17	1.72 ± 0.56	2.12 ± 1.14	3
Rotational	1.8 ± 0.8	0.84 ± 0.09	1.73 ± 1.03	1.24 ± 0.97	2
Buffer strip/crop	2.3 ± 0.6	0.81 ± 0.08	3.50 ± 1.25	0	0

[1] Berger-Parker Index of Dominance.
[2] Continuously grazed, rotationally grazed, and buffer strip within row crop field.
[3] Mean ± standard error.

edges, 24% with wetlands, and 20% with grasslands. Eighty percent of the grassland species observed were species of management concern. Grassland species were defending territories on the pastures and therefore assumed to be using them for breeding, while all other species were only observed feeding in pastures. Species in buffer strips were defending territories. Species occurring in row crops were only observed feeding, with the exception of Killdeer, which were confirmed to be nesting.

Species richness varied between 1.75 to 5.50 species per site over the 3 years and land use types (Table 2). In any 1 year, species richness per site did not differ among continuous pastures, rotational pastures, and buffer strip/crops ($p > 0.25$, all 3 years). Bird density varied between 1.7 to 4.6 birds ha^{-1} over the 3 years and land use types (Table 2). Within a year, total bird density was not different among land use types ($p > 0.25$, all 3 tests).

Within years, dominance indices were similar between the land use types ($p > 0.05$, all 3 tests). On average, over all years and land use types, dominance was 0.56 (Table 2). On the continuously grazed sites, the dominant species was Savannah Sparrow. On the rotationally grazed sites, the dominant species were Savannah Sparrow and Red-winged Blackbird. On the buffer strip/crop sites, the dominant species was Red-winged Blackbird. Species in common between the buffer strip/crop and continuously grazed sites were Red-winged Blackbird and Song Sparrow, found on the majority of sites in all land use types. However, of the 4 grassland species observed (Table 1) in any 1 year, 3 to 4 of the species were seen on the continuously grazed sites, not on the buffer strip/crop sites. In contrast, bird communities on the continuously grazed and rotationally grazed sites had 2 to 3 of the grassland bird species in common.

Densities of species of management concern as a group (Savannah Sparrow, Eastern Meadowlark, Bobolink, and Sedge Wren) were not significantly different between continuous and rotational pastures within years ($p > 0.4$, all 3 tests). This also was true for Savannah Sparrow, the more commonly occurring species ($p > 0.5$, all tests). Only 2 Savannah Sparrows and none of the other species of management concern were seen on buffer strip/crop sites.

Vegetation-bird community relationships

Mean values and standard errors for each vegetation parameter measured are presented in Table 3. Species richness was not related to vegetation structure in 2 of the 3 years (i.e., no model was chosen by step-wise selection in 1997 and 1998). In 1996, species richness had a tendency to be related to vegetation height-density ($R^2 = 0.227$, $P = 0.076$). In this case, there tended to be higher richness on sites with lower vegetation height-density. These tended to be sites with continuous and rotational grazing compared to the buffer strip/crop sites.

Bird density was related to vegetation structure. In 1996 and 1998, there was a higher density of birds with deeper litter depths (1996: $R^2 = 0.379$, $P = 0.033$; 1998: $R^2 = 0.635$, $P = 0.002$). Litter was deeper on buffer strip sites compared to the continuous and rotational sites (Table 3). In 1997, there was a tendency for density to be higher with more bare ground (1997: $R^2 = 0.280$, $P = 0.077$). Buffer strip/crop sites had more bare ground compared to continuous and rotational sites (Table 3).

Density of grassland species of concern was also related to vegetation structure. In 1996 and 1998, there tended to be a higher density of grassland birds on sites with less bare ground (1996: $R^2 = 0.282$, $P = 0.075$; 1998: $R^2 = 0.278$, $P = 0.078$). There

Table 3. Vegetation structure measurements for each land use type within each year of the study (n=4).

Land Use Type	Bare Ground	Litter Depth	Height-density
	-----(%)-----	-----(cm)-----	-----(cm)-----
1996			
Continuous[1]	11.6 ± 2.4	1.1 ± 0.3	9.5 ± 1.9
Rotational	8.7 ± 3.7	1.5 ± 0.6	11.6 ± 3.2
Buffer strip/crop	36.8 ± 1.8	3.5 ± 0.6	26.2 ± 1.2
1997			
Continuous	10.0 ± 2.3	0.7 ± 0.1	4.8 ± 1.3
Rotational	6.0 ± 2.8	1.2 ± 0.4	13.9 ± 2.9
Buffer strip/crop	36.6 ± 2.8	3.2 ± 0.3	24.3 ± 5.3
1998			
Continuous	7.8 ± 1.6	0.7 ± 0.4	9.6 ± 2.6
Rotational	10.9 ± 2.3	2.3 ± 0.8	13.9 ± 2.2
Buffer strip/crop	44.0 ± 2.1	10.0 ± 3.8	38.5 ± 1.7

[1] Continuously grazed, rotationally grazed, and buffer strip within row crop.

was less bare ground on continuous and rotational compared to the buffer strip/crops (Table 3). In 1997, there tended to be higher densities of grassland birds on sites with shallower litter depths ($R^2 = 0.291$, $P = 0.070$). Litter depth tended to be shallower on the rotational and continuous sites compared to the buffer strip/crop sites (Table 3).

Table 4. Comparison of bird communities near (<10 m) and away (>10 m) from stream in continuous and rotational pasture sites (n=4 for each pasture type in each year).

Land Use Type		Species richness	Total Density	Density of species of concern
		----(No. site^{-1})----	----(Birds ha^{-1})----	----(Birds ha^{-1})----
1996	Continuous[1]	--	--	--
	Rotational	--	--	--
	Both pasture types	near < away t=-2.9, df=7, P=0.022	near > away t=2.26, df=7, P=0.06	near ± away t=0.79, df=7, P=0.45
1997	Continuous	near < away 2.5 ± 0.9 < 4 ± 0.9	--	--
	Rotational	near ± away--	--	
	Both pasture types	Interaction F=8, df=1,6, P=0.03	near ± away P > 0.25, all tests	near < away 0.9 ± 0.5 < 6.0 ± 2.3 t=-2.15, df=7, P=0.69
1998	Continuous	-- --	near > away 3.8 ± 1.2 > 1.4 ± 0.7	-- --
	Rotational	--	near ± away	--
	Both pasture types	near ± away P > 0.25, all tests	Interaction F=8.75, df=1,6, P=0.002	near < away 0.6 ± 0.4 < 2.3 ± 1.0 t=-1.98, df=7, P=0.088

[1] Continuously grazed, rotationally grazed, and buffer strip within row crop.

Bird community comparison near and away from stream on pastures

There was some evidence of a difference in species richness near and away from stream on the pastures (Table 4). In 1996, there were fewer species near the stream than away, regardless of pasture type. In 1997, there were differences in species richness near and away from the stream depending on the pasture land use type. Specifically, there were fewer species near the stream than away on continuous pastures; species richness was similar near and away from the stream on rotational pastures. Grassland species were found both near and away from streams, though Bobolink and Eastern Meadowlark were seen only away from the streams (Table 1).

There was no consistent difference in total bird density near and away from stream on the pastures (Table 4). In 1996, there tended to be more birds near the stream than away, regardless of pasture type. In 1998, there were differences in densities near and away from the stream, depending on pasture type. Specifically, on continuously grazed pastures, there were more birds near the stream than away; there was no difference in densities near and away from streams on rotationally grazed pastures.

This pattern differed for grassland species of concern (Table 4). In 1997 and 1998, there tended to be higher densities of grassland species of concern away from the stream, regardless of pasture type.

Differences in species richness between near and away from streams were not related to differences in vegetation structure ($p > 0.25$, all models). There were some differences in bird density related to vegetation structure near and away from streams, but these were not consistent among years. No density differences were related to vegetation structure differences in 1996. In 1997, density differences were related to litter depth differences ($R^2 = 0.632$, $P = 0.02$). Specifically, there were higher densities of birds near the stream when near-stream litter was shallower than away from stream. In 1998, besides being associated with pasture type, density differences were associated with vegetation height-density differences ($R^2 = 0.91$, $P = 0.01$). Specifically, there were higher densities of birds near the stream when vegetation height-density was higher near the stream compared to away from stream.

For grassland species of concern in 1996, density differences tended to be associated with differences in vegetation height-density ($R^2 = 0.409$, $P = 0.088$). Specifically there tended to be more grassland birds near the stream when vegetation height-density was higher near the stream compared to away from streams. No vegetation parameters were associated with grassland bird density differences in 1997. In 1998, differences in bare ground and litter depth were associated with differences in grassland bird densities ($R^2 = 0.706$, $P = 0.03$ for bare ground; $P = 0.053$ for litter depth). In this case, densities of grassland birds were higher near the stream when there was more bare ground or when litter depth was shallower.

Discussion and Conclusions

Species richness, dominance, and density were similar between the 3 land use types. Continuous and rotational pastures supported grassland bird species of management concern: Savannah Sparrow, Eastern Meadowlark, and Bobolink. Sedge Wrens were also found on continuous pastures. With the exception of 2 Savannah Sparrows observed during 1 survey, species of management concern did not occur on the 10-m buffer strips. This is similar to the results of Holmquist (1991), who rarely found Eastern Meadowlarks on ungrazed herbaceous riparian buffer strips located within grazed pastures in Pennsylvania, and found no Savannah Sparrows or Bobolinks despite their presence in the general study area. In contrast, ungrazed grassed waterways of greater width have been shown to support breeding grassland birds such as Savannah Sparrow, Eastern Meadowlark, Bobolink, and Sedge Wren (Robert Howe, Wisconsin Dep. Nat. Resources, 1999, unpubl. report), as well as Western Meadowlark, Dickcissel (*Spiza americana* Gmelin), and Grasshopper Sparrow (Bryan and Best 1991). Unlike the riparian buffer strips in this study, however, grassed waterways are non-riparian grassy strips located in upland crop fields, rather than in lowland areas along streams, which may account for the differences between this study and those conducted in grassed waterways. Linear grassland habitats, such as road rights-of-way, of similar width to the buffer strips and also surrounded by crop fields, can support species of management concern such as Eastern and Western Meadowlarks, Sedge Wren, Dickcissel, and Savannah Sparrow (Warner 1992, Camp and Best 1993). Buffer strips in this study may have been unsuitable for species of management concern because of their extremely dense, tall vegetation, steep streamside slopes, potential for flooding, limited width, location within unsuitable row crops, the presence of scattered shrubs, or a combination of these factors.

Overall bird density was related to vegetation structure, with higher densities located on sites with deeper litter. This result was partially driven by the buffer strips, which had higher bird densities and greater litter depth than the pastures. It is interesting to note that litter depths were high enough in buffers to more than compensate for the abundance of litter depth values of 0 found in adjacent row crops, yielding overall higher litter depth values than in pastures. Positive correlations between bird density and litter depth have been found in previous studies of similar bird communities (Sample 1989, Wiens and Rotenberry 1981).

Density of species of management concern tended to be negatively correlated with bare ground. This result was driven by buffer strip/crop sites, which had very high proportions of bare ground in the cropland and few species of management concern. Grassland bird densities have been found to be negatively correlated with bare ground in other studies (Sample 1989, Wiens 1974).

Within the pastures in our study, there was no consistent influence of proximity to streams on overall species richness, density, or dominance. There was a trend for grassland birds of management concern to differ in occurrence and density near and away from streams in pastures. These species tended to occur more frequently and at higher densities away from the stream, regardless of pasture management. These results differ from studies conducted in forest and shrub species in western (Anderson et al. 1994, Knopf 1985), southwestern (Medin and Clary 1991, Stahlecker et al. 1989, Szaro 1981), and Great Plains (Lowther 1984, Stauffer and Best 1980, Tubbs 1980) riparian areas, which found higher bird species richness and/or density in riparian areas than in other habitats in general. In contrast to the previous studies, the vegetation structure adjacent to the pasture streams in our study does not differ dramatically from the structure in the rest of the pasture.

Densities of all species as well as species of management concern showed the same patterns in relation to vegetation near and far from streams in pastures. Specifically, densities tended to be higher near streams when the litter depth was lower and vegetation height-density was higher than away from streams. These results differ from most other studies on grassland birds in non-riparian habitats. In 1 Wisconsin farmland study (Sample 1989), grassland bird density was positively correlated with moderate litter and negatively correlated with vegetation height-density and low litter. Wiens (1974) evaluated grassland bird-vegetation relationships on a continental scale and found a tendency for greater bird densities to be associated with areas with greater litter depth and grass cover and less bare ground. Rotenberry and Wiens (1980) found the same relationships for eastern tallgrass species (Grasshopper Sparrow, Dickcissel, and Eastern Meadowlark). Comparisons with other studies are difficult, however, since correlations reflect the habitat chosen relative to habitat availability in the study area.

We found that pastures, regardless of type of management, supported higher average densities of grassland species of concern than buffer strip/crops. We also found no difference in grassland bird density between continuously and rotationally grazed pastures. This finding differs from the results of a previous study in the same region of Wisconsin (Temple et al. 1999). In their study, the same grassland species of concern (Sedge Wren, Savannah Sparrow, Eastern Meadowlark, and Bobolink) were more abundant on rotationally grazed pastures than continuously grazed pastures. This discrepancy may be due to differences in the types of sites evaluated. Although both studies were conducted within the Driftless Area of southwestern Wisconsin, this study evaluated riparian lowland pastures, whereas the study conducted by Temple et al. (1999) evaluated upland pastures. There is evidence that some grassland species of management concern occur more frequently and/or at higher density in upland pastures than in lowland pastures (Renfrew 1999).

Another possible explanation for the discrepancy is that the vegetation structure in continuous pastures appears to have been different between this study and that of Temple et al. (1999). Continuous pastures in Temple et al. (1999) had “little vegetative cover and were kept closely cropped by cattle”. In contrast, some of the continuous pastures in this study were not heavily grazed and supported Sedge Wrens, a species known to avoid short grass. Heavy grazing that maintains low vegetative cover and height-density is generally less favorable to grassland birds of management concern than light or moderate grazing (see Bock et al. 1992, Herkert et al. 1996, and Swanson 1996 for a review). The continuous pastures in this study likely represented more moderate stocking rates than Temple et al. (1999), which may explain our different conclusions. The stocking rates selected for a study may heavily influence results when comparing continuous grazing to other grazing treatments or land uses.

It is clear that pastures provided better habitat for grassland bird species of management concern than 10-m-wide buffer strip/crops. Therefore, if management is focused on these species, pastures should be favored over 10-m-wide ungrazed buffer strips along streams located within row crop fields. Research has not yet been conducted to determine how wide buffer strips should be to benefit grassland birds (D. Sample, Wisconsin Department of Natural Resources, pers. comm.). Because grassland bird species of management concern tend to occur at lower densities adjacent to streams, management decisions that affect land use at the scale of the farm are likely to have a much greater impact on these species than stream management decisions affecting only the immediate riparian area.

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Economics of managing mesquite in north Texas: a sensitivity analysis

W. R. TEAGUE, R.J. ANSLEY, U.P. KREUTER, W.E. PINCHAK, AND J.M. McGRANN

Authors are associate professors, Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, Tex. 76385, assistant professor Department of Rangeland Ecology and Management, Texas A&M University, College Station, Tex. 77843-2126, associate professor, Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, Tex.76385, and professor Department of Agricultural Economics, Texas A&M University, College Station, Tex. 77843-2124.

Abstract

This paper presents a comparative simulation analysis of the economics of prescribed fire and aerially applied root-killing herbicide treatment as methods for maintaining livestock productivity on rangeland in the Texas Rolling Plains. A “no-treatment” scenario is used as the base for comparison. In almost all the simulated scenarios both herbicide application and prescribed burning were economically feasible since net present values were > 0 and benefit/cost ratios were >1. However, the net present values for prescribed fire were much higher that those for the herbicide treatment even with a lower increase in carrying capacity with burning. The cost of herbicide would have to be less than half the current cost of $57 ha^{-1} before it would be economically competitive with fire in controlling mesquite. If cattle numbers were not increased after treating brush, burning had an even greater net present value and benefit/cost ratio advantage over herbicide treatment than if cow numbers were increased after treatment. Even if fences have to be constructed to implement adequate deferment for burning, the net present value and benefit/cost ratios of the fire option were higher than those for herbicide scenarios. This analysis indicates that there is an economic advantage to using fire wherever possible, and use of herbicides is restricted to those instances when fine fuel amount is < 1,700 kg ha^{-1} yr^{-1} when fire is not a viable option. The analyses indicate the economic response is most sensitive to the treatment effect on wildlife income.

Key Words: Brush management, bioeconomics, natural resource accounting, prescribed burning, root-killing herbicide

Resumen

Este artículo presenta un análisis de simulación comparativo del aspecto económico del fuego prescrito y los tratamientos de aplicación aérea de herbicida como métodos para mantener la productividad del ganado en pastizales de la región de las Planicies Onduladas de Texas, se uso un escenario "Sin Tratamiento" como base de comparación. En casi todos los escenarios simulados la aplicación de herbicida y el fuego prescrito fueron económicamente factibles ya que los valores netos presentes fueron > 0 y las relaciones beneficio/costo fueron > 1. Sin embargo, los valores netos presentes para el fuego prescrito fueron mucho mayores que los del tratamiento de herbicida, aun con un menor incremento en la capacidad de carga debida al fuego. El costo del herbicida tendría que ser menos de la mitad del costo actual de $57 ha^{-1} antes de que fuera económicamente competitivocon el fuego para controlar mezquite. Si los números de ganado no se incrementaron después de tratar los arbustos, la quema aun tendría un mayor valor neto presente y una ventaja en la relación beneficio/costo sobre el tratamiento con herbicidas que si los números de ganado se incrementaran después del tratamiento. Aun, si se tiene que construir cercos para implementar un diferimiento adecuado de la quema, el valor neto presente y la relación beneficio costo del fuego fueron mayores que las de los escenarios con herbicidas. Este análisis indica que hay una ventaja economica para usar el fuego cuando sea posible, y el uso de herbicidas se restringe a aquellas ocasiones cuando la cantidad de combustible fino es < de 1,700 kg ha^{-1} año^{-1}, cuando el fuego no es una opción viable. El análisis indica que la respuesta económica es mas sensitiva al efecto del tratamiento en el ingreso por fauna silvestre.

In the southwestern U.S.A., honey mesquite (*Prosopis glandulosa* Torr.) dominates many rangelands reducing herbaceous production and interfering with livestock foraging and management. The accelerated increase of woody plants into grasslands has been attributed to overgrazing and lack of fire (Scifres 1980). Traditionally, mesquite rangelands have been managed for beef cattle production but increasingly income from wildlife can equal or exceed that from livestock on many ranches (Bernado et al. 1994). The cost to control mesquite, the cost of follow-up maintenance treatments and the net earnings of the treated versus non-treated land determine the economics of brush control. Previous research by Vantassell and Conner (1986) recognized the response from treatment but ignored the fact that if brush is not controlled it increases. This further reduces herbage production, increases cattle management costs, and may reduce wildlife earning capacity.

This paper presents the difference in net present value and benefit/cost (B/C) ratios for treating mesquite using 2 of the most cost-effective brush management treatments in the Rolling Plains of Texas: prescribed burning at an interval of 5—7 years and aerial spraying with a root-killing herbicide that has a treatment life of approximately 20 years (Scifres and Hamilton 1993, Ueckert et al. 1999). The biological information used in these calculations was collected from small-scale independent projects in the

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Rolling Plains of Texas. Since this database is incomplete, a sensitivity analysis was conducted to identify the relative importance of the different biological and economic parameters needed to develop biologically and economically sustainable management systems. The analysis relates to ranches that are 1,600 to 20,000 ha in size with mesquite that needs a brush reduction treatment. The costs and benefits of carrying out particular management actions are compared with the value in lost productivity due to not treating the brush.

Methods and Procedures

Economic model

The economic efficiency of treating brush with fire or herbicide was calculated by determining the differences in net present value and benefit/cost ratio of treated vs. untreated land over a 30-year period. A project is considered economically feasible if net present value ≥ 0 (i.e. discounted returns exceed discounted costs). Treatments with higher net present value ratios are considered economically superior (Workman 1986). The benefit/cost ratio was calculated by determining the difference in present value of returns (benefits) divided by the present value of treatment costs and maintenance. The ratio must be greater than 1 for the treatment to be economically feasible.

The change in land value is not taken into account because land values are often unrelated to productivity and are frequently driven by speculative investors. Calculation of net present value was as follows:

$$\mathrm{NPV} = \sum_{i=0}^{n} R_i/(1+d)^I \qquad \textbf{(1)}$$

Where R = future net value
d = discount rate or rate of return
n = planning horizon
i = years

In the economic model, carrying capacity was calculated for each year of the analysis by multiplying average carrying capacity per hectare by the number of hectares. The total lease value was estimated by multiplying the carrying capacity by the lease rate. The net present value of each treatment was calculated using a 30-year time horizon of treatment benefits and costs and a specified discount rate. The analyses were based on the assumption that income and operating costs are incurred at the end of each year, with the exception of initial treatment costs, which were assumed to occur at the beginning of year 1. The analyses were conducted using a spreadsheet program developed by McGrann et al. (1998). Costs of the treatment and maintenance were entered into the spreadsheet, as well as any associated improvements (fencing, water, facilities, etc.), using data from the Waggoner Experimental Ranch in north Texas (33° 50' N, 99° 5' W). Since net present value and benefit/cost ratio estimates are correlated, we discuss only the net present value of each treatment analyzed. However, in the associated tables, benefit/cost ratios are also presented to accommodate preferences for either measure. Analysis showed little sensitivity to a range of discount rates so a rate of 5% was used. We used the current rate for leased cow-calf ranchland in the Rolling Plains of Texas of \$90 Au^{-1} year^{-1} (Stan Bevers, Extension Economist, TAEX, Vernon, Tex., personal communication).

Grass production with increasing brush

Treatment response and longevity have a major effect on the economic efficacy of brush clearing. Herbage growth beneath mesquite changes little until a threshold is reached beyond which herbage growth is severely reduced (Dahl et al. 1978). An increase in herbage with clearing was only obtained if pre-treatment mesquite cover was 30% or more (Dahl, et al. 1973). The magnitude of herbage growth response following clearing also differed markedly depending on climatic conditions, the productive potential of the soil and the herbage species composition or range condition at the time of treatment (Dahl et al. 1973, Scifres and Polk 1974, McDaniel et al. 1978, 1982, Brock et al. 1978, Gibbens et al. 1986).

Recent work in north Texas has defined the long-term regrowth and invasion of mesquite following a root-killing herbicide and the resulting reduction of herbage production as mesquite aerial cover increased over a 30-year period, summarized in Fig. 1. Mesquite cover was estimated to increase at a rate of 1 percentage unit per year (Ansley et al. 2001). Carrying capacity was calculated using the percentage reduction in herbage production due to mesquite from McMullen (2000) and the mean herbage production from 5 years of field data in north Texas (Teague et al. 1999). Allocating 25% of peak standing crop at 12 kg Au^{-1} day^{-1}, these calculations give an average carrying capacity for Waggoner Experimental Ranch of approximately 12.1 ha AUY^{-1}. The Waggoner Experimental Ranch is stocked at 13.4 ha AUY^{-1} for average precipitation years (Teague et al. 1999). This research area comprises approximately equal proportions of shallow-clay soils that have very low amounts of mesquite and clay-loam soils that support significant mesquite cover. The shallow-clay soils currently have a carrying capacity of approximately 15.8 ha AUY^{-1} (Table 1). The clay-loam soils have a carrying capacity of approximately 8.9 ha AUY^{-1} when clear of mesquite and 13.4 ha AUY^{-1} with 30% aerial cover of mesquite.

The assumed changes in productivity (carrying capacity) with time following no-treatment and treatment are presented for prescribed fire (Fig. 2) and are based

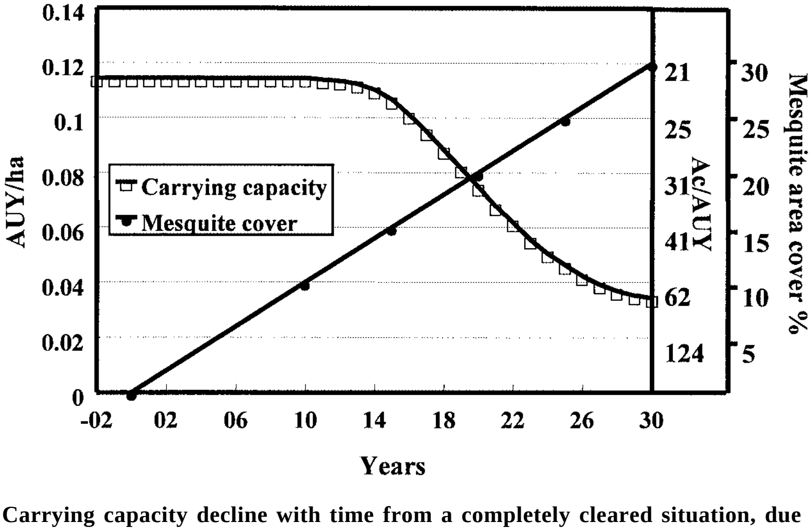

Fig. 1. Carrying capacity decline with time from a completely cleared situation, due to increasing mesquite brush on the Waggoner Experimental Ranch (from McMullen 2000, Ansley et al. 2001).

Table 1. Parameter values used in the economic analyses.

	Parameter	Herbicide	Fire
1	Area to be treated (%)	50	50
2	Mesquite aerial cover before treatment (%)	30	30
3	Discount rate (%)	5	5
4	Income tax rate (%)	15	15
5	Capital gains tax rate (%)	20	20
6	Wildlife income ($ ha^{-1})	7.41	7.41
7	Treatment longevity (years)	20	7
8	Cost [$ ha^{-1}] Initial treatment	56.81	6.18
	Follow-up treatments	6.18	6.18
9	Carrying capacity untreated area (ha AUY-1) *	15.8	15.8
10	Carrying capacity of treated area before treatment (30% mesquite)**	13.4	13.4
11	Carrying capacity of treated area after treatment (10% mesquite)**	8.7	10.9

*Land that has shallow-clay soil of relatively low productivity for herbage and very low amounts of brush. Carrying capacity has been calculated by allocating 25% of peak standing crop @ 12 kg hd^{-1} day^{-1} using 5 years of data from Teague et al. (1999).

**Land that has clay-loam soils of moderately productive soils where the major presence of mesquite occurs. Carrying capacity has been calculated as above.

on results for north Texas in which top-killing treatment effects lasted 6 to 7 years (Heitschmidt et al. 1986). We assume that fire would need to be applied once every 7 years to suppress mesquite regrowth. Grass growth the season after fire was assumed to be at pretreatment levels. One scenario we considered was that the peak production after year 1 increased with repeated fires as illustrated in Fig 2. We also considered a reduced response in which the lower peak production following the first burn in Fig. 2 occurred after all burns in the 30 year period. We also considered scenarios with no response delay and burning every 5 years compared to every 7 years.

Twenty-year and 30-year longevity scenarios are considered following herbicide application with no follow-up treatment (Fig. 3) based on data in which root-killing treatment effects lasted up to 20 years (Ansley et al. 2000). In addition, 2 alternative scenarios are considered following herbicide application with the 20-year return to pretreatment levels (Fig. 4). These include follow-up treatment with prescribed fire 16 or 20 years after the initial herbicide application.

The parameter values used for the majority of scenarios are presented in Table 1. The current recommendation for herbicide application to control mesquite on large ranches is to aerially broadcast 0.28 + 0.28 kg ha^{-1} Clopyralid + Triclopyr herbicide at a cost of $57 ha^{-1} (Ueckert et al. 1999). Although technology has been developed to treat individual mesquite plants at a much lower cost of $30 ha^{-1} for densities of 1,000–1,200 plants ha^{-1} (Ueckert et al. 1999), this method of application is generally applicable only for smaller scale properties and was thus not used for these large ranch simulations.

Costs of burning in north Texas, including the cost of creating firebreaks and pre-burning blacklines range from $6 to $7 ha^{-1} (Ansley et al. 1999). However, it is possible to burn at lower cost if pre-burn preparations only include the cost of grading the perimeter of the area to be burned. For most scenarios a retreatment interval of 7 years is used for burning but in 1 scenario a retreatment interval of 5 years is considered. The same cost ha^{-1} was used for each repeat burn. We assume pre- and post-burn deferment.

All scenarios assume that cattle numbers will be increased according to the increase in herbage production following brush treatment. However, cattle numbers are not increased on some ranches. In such cases, individual cow production would increase owing to the increased amount of

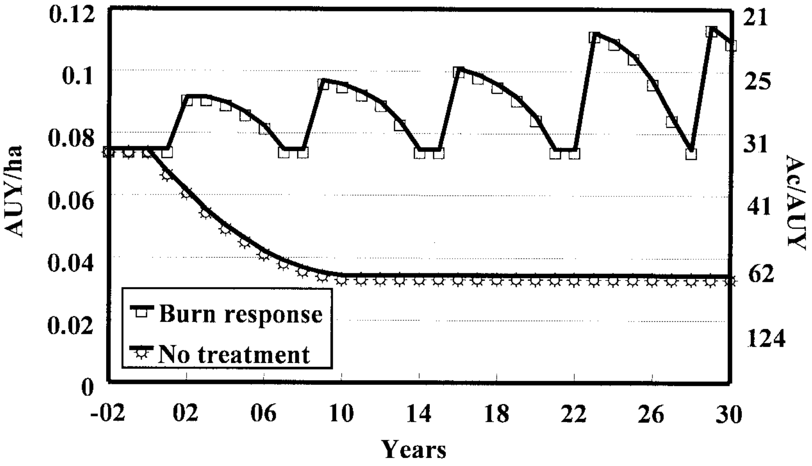

Fig. 2. Carrying capacity of treated compared to untreated mesquite using prescribed burning. Grass growth the season after fire was assumed to be at pretreatment levels. The peak production after year 1 was assumed to increase with repeated fires.

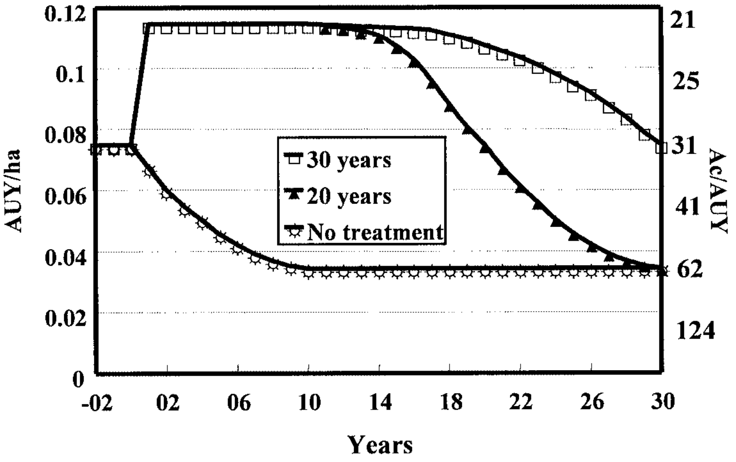

Fig. 3. Carrying capacity of treated compared to untreated mesquite using a root-killing herbicide with treatments lasting 20- and 30-years before pretreatment levels are reached.

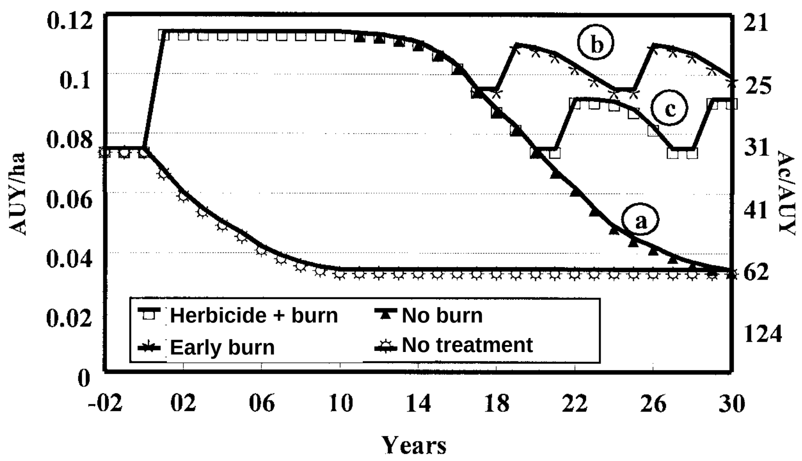

Fig. 4. Carrying capacity of treated compared to untreated mesquite using a root-killing herbicide followed by different post-herbicide treatment prescribed burn scenarios: (a) no burning (b) burning after 16 years and (c) burning after 20 years.

herbage per cow as demonstrated by Bement (1969). The option of not increasing cow numbers following brush treatment was compared to the option of increasing cow numbers to use extra herbage produced using increased individual cow performance of 5 and 10% following treatment if cow numbers remained static. This is based on annual fluctuations in animal performance of 5-10% measured in north Texas due to varying amounts of herbage produced in response to climatic variability and different stocking rates (Heitschmidt et al. 1986, Teague et al. 1999). We assume that using light to moderate stocking rates will prevent having to reduce stock numbers in times of serious drought.

Factors affecting the efficacy of herbicides and burning

Uncertainty exists about how effective fire can be relative to herbicide application in reducing the problems associated with mesquite. This sensitivity analysis aims at determining which factors and combinations of factors significantly influence the relative economic value of these alternative treatments. Burning has a significant effect on environmental conditions, which lasts a number of years (Wright and Bailey 1982). The removal of surface and standing litter by fire and the blackened soil surface result in higher soil temperature. This promotes growth earlier in spring and increases soil moisture evaporation, both of which reduce soil moisture more rapidly. The increase in herbage quality and increase in number of species that are consumed after burning (Wright and Bailey 1983) counteract the reduced amount of herbage produced. The net result is that secondary productivity can be increased on burned relative to unburned areas when favorable growing conditions prevail (Angell et al. 1986, Svejcar 1989). However, primary and secondary productivity are reduced on burned areas when growing conditions are below average (Wright and Bailey 1982). We do not know how many years these areas take to recover. However, in a study in the Rolling Plains of Texas with rotational grazing, the number of grazing days was doubled in burned pastures, compared to non-burned pastures, in years 2 and 3 after burning (Teague et al. 1999) when burning was followed by a drought year.

Fire generally results in patchier and less complete canopy top-kills than broadcast herbicide application, resulting in less reduction in brush aerial cover and lower increase in herbage production with prescribed fire (Hamilton et al. 1981). The longevity of treating mesquite with fire appears to be similar to that reported above for top-killing herbicides. In the case of mesquite in the Rolling Plains, retreatment is necessary after approximately 6 to 7 years, based on work by Heitschmidt et al. (1986), but retreatment may be needed after only 5 years since few mesquite are killed even with repeated fires (Ansley et al. 1998).

Pre- and post-burn deferments are necessary to minimize the negative environmental effects of fire and to provide adequate amounts and continuity of grass fuel (Scifres and Hamilton 1993, Teague et al. 1997). One-herd multiple-pasture systems facilitate such deferment and allow the use of fire in non-drought years at a frequency of 4 to 6 years to internalize the cost of treating the brush by avoiding the cost of grazing extra land. Most ranches would be able to implement at least a 4-pasture, 1-herd system of management without incurring extra fencing costs by consolidating herds. However, scenarios that do require extra fencing to implement deferment are considered in this economic analysis to account for this possibility. The economic consequences of adding electric or regular 5-wire fencing in year 1 are considered using costs of $210 and $2,100 per kilometer of fence, respectively. In addition, assuming that 1/4 of the grazing unit will be deferred and burnt, approximately 10% of total grazing days in a year are lost due to deferment. This would result in a small loss in animal productivity since the effective stocking rate would be heavier and animals would not perform as well. Burning 1/8 of the grazing unit would result in losing 5% of total grazing days and would be managed for with a burning interval of 7–8 years. We consider a scenario in which 10% fewer animals are stocked to determine the economic consequences of decreasing animal numbers to account for the days of lost grazing. We assume that no post-treatment deferment is necessary following herbicide application based on Ueckert et al. (1999).

Wildlife and brush clearing

Wildlife is an increasingly important addition to ranch income (Bernado et al. 1994). Wildlife requires suitable cover and food plants to satisfy habitat requirements. For example, optimal habitat for bobwhite quail and white-tailed deer includes about 10–20% brush cover (Lehman 1984, Guthery 1996, Teer 1996). Thus any management practice that influences habitat for these species will change income derived from them. Herbicides and fire affect deer and quail habitat differently. While complete clearing with herbicides may be desirable for livestock production it would significantly reduce the value of the area for deer and quail. However, patterns of clearing can be implemented using herbicides that optimize cover requirements for specific species (Fulbright and Guthery 1996, Koerth 1996). After herbicide treatment aimed at reducing brush, forb populations important for deer and quail are generally suppressed for at least 1 growing season. However, forb abundance can improve significantly in treated areas in subsequent years (Scifres and Koerth 1986, Koerth 1996).

Burning can have a positive effect on wildlife habitat for some species. Burns improve plant composition and the quality of feed for many wildlife species and thus attract wildlife (Guthery 1996, Teer 1996). Early winter burning has been shown to increase forbs that are significant to white-tailed deer (Hansmire et al. 1988). In addition, at the landscape level the patchy nature of fires leaves islands of cover that enhance habitat. Woody plants also regrow rapidly after top-kill by fire and provide cover more rapidly than root-killing herbicide applications. Small amounts (<15% cover) of woody plant cover interfere little with livestock management for 3 to 4 years after a burn and provide relatively little competition with herbage production (McMullen 2000). The changes in grazing management required to provide pre- and post-burning deferment have also been shown to improve habitat for wildlife. For example, at the Sonora Experiment Station in south Texas, White-tailed deer preferred a 7-pasture-1-herd cattle grazing rotation system over the 4-pasture-3-herd deferred and continuous graze systems (Reardon et al. 1978).

The consequences of increasing or decreasing income from wildlife are considered using a wildlife income of \$7.41 ha-1 for the whole management unit. This is the wildlife income level used by Thurow et al. (2000) for brush at 5 to 15% aerial cover. Wildlife income is increased or decreased to the upper (\$12.35 ha^{-1}) and lower (\$2.47 ha^{-1}) levels likely to be encountered in north Texas (Dr. Dale Rollins, Wildlife Extension Specialist, TAEX, San Angelo, Tex., personal communication) on the treated portions of the management unit to simulate positive or negative effects on wildlife income that may occur with either method of treating the brush.

Results and Discussion

In almost all the simulated scenarios both herbicide application and prescribed burning were economically feasible since net present values were >0 and benefit/cost ratios were >1. However, the net present values for prescribed fire were much higher than those for the herbicide treatment (Table 2). The lowest net present values were for the herbicide with herbicide follow-up treatment. When the herbicide with a follow-up burn after 20 years was compared to the burn with a delayed response, net present value remained much higher for the prescribed burn treatment. When the longevity of the herbicide was assumed to be 30 years, net present value increased relative to the 20-year longevity but the net present values for prescribed fire were still higher.

Table 2. Consequence of treating mesquite with root-killing herbicides or prescribed fire on net present value (NPV) and benefit/cost (B/C) ratio under different management scenarios.

Treatment	Treatment Longevity	Scenario Description	Treatment Cost		NPV	B/C Ratio
			Initial	Follow-up		
			--------- (\$ ha^{-1})--------			
Herbicide	20 years	No follow-up burn	56.81	0	12.2	2.3
	30 years	No follow-up	56.81	0	14.8	2.5
	20 years	Follow-up burns after 16 years	56.81	6.18	13.6	2.3
	20 years	Follow-up burns after 20 years	56.81	6.18	13.2	2.3
	20 years	Herbicide after 20 years	56.81	56.81	11.0	1.8
Burn	7 years	Response delayed 1 year	6.18	6.18	18.0	6.8
	7 years	Response not delayed	6.18	6.18	18.5	7.0
	7 years	10% fewer animals	6.18	6.18	16.2	6.8
	7 years	Reduced response	6.18	6.18	17.3	6.6
	5 years	Response not delayed	6.18	6.18	15.7	4.4

Net present values of burn scenarios which considered reduced stock numbers and reduced carrying capacity increase following fire were still much higher than those of the herbicide with follow-up burn treatments (Table 2). With the scenario of no delayed response following a burn, a slightly higher net present value was realized compared to the delayed response. The scenario of burning at 5-year intervals lowers net present value values relative to the 7-year burn interval but still has greater net present value than the herbicide scenario. The option of burning 16 years rather than 20 years after herbicide application did not increase net present values. In practice, this strategy would probably be advisable since there would be a greater certainty of applying effective burn treatments with lower levels of brush. The longer retreatment is delayed the higher the amount of brush and the lower the amount of fuel to carry fire to achieve adequate brush control. This would be accentuated during drought years.

The main reason for the low net present value values when using herbicide is the high initial cost of application. Low net present values were associated with early, large capital expenditures compared to the same amount spent over the length of any period under examination. The high net present values for prescribed burning were a result of a number of small investments spread over the 30-year period compared to the large single investment at the beginning for herbicide application.

The option of not increasing cow numbers after treating mesquite is considered in Table 3. All scenarios were economically feasible and all net present values were greater for burning than herbicide scenarios. In addition, with the herbicide options, the net present values for maintaining constant cow numbers were 68 to 72% those of the option for increasing cow numbers. In contrast, with the burning options, the net present values for maintaining constant cow numbers were 89 to 92% those for increasing cow numbers. Therefore, if cow numbers are not increased after treating brush, burning has an even greater economic advantage over herbicide treatment than if cow numbers are increased after treatment.

It is important to indicate that the results

Table 3. Net present value (NPV) and benefit/cost (B/C) ratio consequences of treating mesquite with root-killing herbicides or prescribed fire under different management scenarios: (1) increasing cow numbers according to the increase in herbage production or (2) not changing cow numbers, and thereby increasing production per cow by 5 or 10%.

Treatment	Scenario Description	Increase in Production Per cow	NPV	B/C Ratio
		(%)	(\$ ha^{-1})	
Herbicide	Increase in cow numbers	0	13.2	2.3
	No Increase in cow numbers	5	9.0	1.9
	No Increase in cow numbers	10	9.5	1.9
Burn	Increase cow numbers	0	18.0	6.8
	No Increase in cow numbers	5	16.0	6.2
	No Increase in cow numbers	10	16.5	6.4

involving prescribed burning in this paper refer only to those circumstances where fine fuel amount is ≥ 1700-kg ha^{-1} yr^{-1} (Ansley and Jacoby 1998). In circumstances where the fuel is less than this, due to the presence of brush or poor herbaceous composition, low site production potential, drought or grazing, the use of prescribed fire to topkill the brush is not possible. In these circumstances other means, such as herbicide application or mechanical brush removal, are usually necessary to restore herbaceous productivity before fire is a viable management option.

Table 4. Consequence of varying the cost of treating mesquite with root-killing herbicides or prescribed fire on net present value (NPV) and benefit/cost (B/C) ratio.

Treatment	Treatment Cost		NPV	B/C Ratio
	Initial	Follow-up		
	---------($ ha^{-1})---------			
Herbicide	56.81	6.18	13.2	2.3
	41.99	6.18	15.8	3.0
	29.64	6.18	17.9	4.1
Burn	12.35	6.18	14.9	3.4
	6.18	6.18	18.0	6.8
	4.94	4.94	18.6	8.6

Table 5. Effect on net present value (NPV) and benefit/cost (B/C) ratio of treating mesquite with root-killing herbicides or prescribed fire if fences have to be erected.

Treatment	Type of Fence	Cost		4 pasture system		8 pasture system	
		4 pasture system	8 pasture system	NPV	B/C Ratio	NPV	B/C Ratio
		----($ ha^{-1})----		($ ha^{-1})		($ ha^{-1})	
Herbicide	None	0	0	13.2	2.3	13.2	2.3
	Electric	1.09	2.62	13.0	2.2	12.8	2.2
	5 wire	9.26	22.23	11.7	2.0	9.4	1.7
Burn	None	0	0	18.0	6.8	18.0	6.8
	Electric	1.09	2.62	17.8	6.5	17.5	6.0
	5 wire	9.26	22.23	16.4	4.5	14.2	3.1

Table 4 illustrates the consequence of reducing the cost of applying herbicides. The cost of the herbicide has to halve to $30 ha^{-1} before net present values for the herbicide are competitive with $6 or $12 ha^{-1} for prescribed burns. However, even at an herbicide cost of $30 ha^{-1}, benefit/cost ratios for burns were greater even at twice the cost ($12 ha^{-1}) of burning measured in field experiments. This analysis showed more sensitivity to cost of herbicide than to treatment longevity following herbicide treatment (compare Table 2 and Table 4).

The cost of adding fences to facilitate pre- and post-burn deferment decreased net present value a small amount if electric fencing is used (Table 5), but using 5-wire fencing reduced economic benefits considerably. In both cases, economic returns are decreased considerably more when herbicides were used instead of fire. Even if a no-fence herbicide scenario is compared with a 5-wire-8-pasture system, the prescribed burning scenario had a greater net present value than the herbicide option. The most likely and economically rational scenario, burning with a 4-pasture or 8-pasture system without incurring any fencing costs, has considerably higher net present values than all herbicide alternatives considered. It should be noted, however, that mesquite density is never reduced with fire, but periodic burning should keep mesquite suppressed.

The importance of improving or decreasing wildlife income with either means of treating mesquite is presented in Table 6. Of all factors considered, net present values show by far the greatest sensitivity to variations in wildlife income. If treatment on any part of a ranch either increases or decreases wildlife income, net present values are changed markedly.

Conclusions

Over a 20 to 30 year period, not treating mesquite brush leads to levels of brush cover that reduce herbage production and hinder normal ranch functions such as gathering cattle for branding and weaning. Once this situation occurs, profitability of livestock production from rangeland is greatly reduced and a large expenditure of capital is usually required for ranchers to continue making a living with livestock.

Clay-loam range sites generally make up 40–60% of the land area in the Rolling Plains of Texas and if left untreated, there is a substantial annual increase in the aerial cover of mesquite on these areas. This poses a significant economic burden to anyone attempting to derive a livelihood from ranching with livestock. Fire, which can be applied at a cost of about $ 6 ha^{-1} or less, is less expensive than spraying with a root-killing herbicide at $ 42 to $ 62 ha^{-1} or mechanical clearing at $124 to $222 ha^{-1}. Prescribed fire has an economic (net present value) advantage over broadcast application of herbicides because of the high initial cost of applying herbicides. This advantage holds even if we assume that fire performs less adequately than herbicides, including a delayed increase in herbage production 1 year after burning rather than the first year after treatment, and an improvement in carrying capacity which is less than that with herbicide treatment. Even with the lowest likely response in carrying capacity with prescribed burning, it compares very favorably in net present value terms, with the current herbicide alternative described above. If cow numbers are not increased after treating brush, burning has an even greater economic advantage over herbicide treatment than if cow numbers are increased after treatment.

The analyses indicate the economic response is most sensitive to the treatment effect on wildlife income since the added income from wildlife is assumed to account for any additional cost. Although

Table 6. Effect on net present value (NPV) and benefit/cost (B/C) ratio of root-killing herbicides and prescribed fire if mesquite removal reduces or improves income from wildlife.

Treatment	Wildlife lease		NPV	B/C Ratio
	Untreated area	Treated area		
	----------------------------($ ha^{-1}yr^{-1})----------------------------			
Herbicide	7.41	7.41	13.2	2.3
	7.41	2.47	[–12.9]	[–0.2]
	7.41	12.35	39.4	4.8
Burn	7.41	7.41	18.0	6.8
	7.41	2.47	[–8.2]	[–1.7]
	7.41	12.35	44.1	15.3

fires are patchier and less effective on larger mesquite than broadcast herbicide application, this would be beneficial if wildlife were part of the equation.

The cost of herbicide would have to be less than half the current cost before it would be economically competitive with fire as a means of controlling mesquite. It should be noted that on smaller properties with less dense mesquite, the use of individual plant treatment using herbicide (Ueckert et al. 1999) might reduce the economic disparity between herbicide and fire treatments as part of a fire plan.

Even if fences have to be constructed as part as a fire plan, the net present value of the herbicide option was lower than those for realistic burning scenarios. Most ranches would be able to implement at least a 4-pasture-1-herd system without any increase in fencing. In addition, grazing systems also have the potential of improving range condition (Norton 1998, Teague et al 1999) and hence primary and secondary productivity. Improving range condition applies to both herbicide and fire treatment and would further improve long-term economic benefits.

Fire is not as easy or convenient to use as chemical or mechanical treatments for controlling mesquite, but it does offer the opportunity of lowering costs substantially by substituting management for capital inputs to increase profit margins. In times of below average rainfall, burning can be very difficult or impossible to implement. Reducing stock numbers and only burning 1/8 of the grazing management unit each year would help considerably in ensuring regular burns were possible in all but abnormally dry years. These analyses show that such management would be very competitive economically with any large-scale herbicide treatment on large ranches. Fire cannot replace herbicides since there are times when herbicides are the only option. This analysis indicates that there is an economic advantage to using fire wherever possible and restricting use of herbicides to those instances that fire is not a viable option. Diversification in the form of adding or increasing wildlife income appears to offer the highest economic return whichever method of mesquite treatment is used.

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Resilience of prickly burnet to management in east Mediterranean rangelands

A. PEREVOLOTSKY, G. NE'EMAN, R. YONATAN, AND Z. HENKIN

Authors are research scientist (A.P.) and field technician (R.Y.) with the Dept. of Natural Resources, Agricultural Research Organization-The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel; Senior teacher (G.N.), Dept. of Biology, University of Haifa at Oranim, Tivon 36006, Israel; and research scientist (Z.H.), Galilee Technological Center (MIGAL), Qiryat Shemona, Israel.

Abstract

Large areas of rangelands in the east Mediterranean Basin are dominated by dense cover of the unpalatable, dwarf shrub prickly burnet (*Sarcopoterium spinosum* (L.) Spach.). This study examined the effectiveness of various shrub control treatments (mechanical removal, chemical/2,4-D control, prescribed burning), combined with NPK fertilization, to reduce shrub cover and encourage the growth of palatable herbaceous vegetation. Chemical control was the most effective treatment, reducing prickly burnet cover to 40% of the initial level 2 years after treatment. Mechanical removal maintained shrub cover at 60% of the initial level, whereas the effect of fire was not detectable after 2 years. Annual and perennial herbaceous vegetation cover was negatively correlated with shrub cover. Fertilization had no effect on the cover of the vegetative components, but increased biomass on the herbaceous patches by 25–240%, depending on the treatment. Our results demonstrate the exceptionally high resilience of prickly burnet growing on chalk substrate to disturbance or attempted eradication, thus rendering most of the tested management options highly ineffective. Effective improvement of rangeland dominated by prickly burnet requires, most probably, a combined treatment including removal of mature shrubs, suppressing their recovery, and stimulating the competing grass component.

Key Words: Shrub encroachment, Mediterranean ecosystem, fertilization, fire, range improvement, *Sarcopoterium spinosum*

Resumen

Grandes áreas de pastizal del este de la cuenca del Mediterráneo están dominados por una cubierta densa del arbusto enano y no apetecido “Prickly burnet” (*Sarcopoterium spinosum* (L.) Spach.). Este estudio examina la efectividad de varios tratamientos de control de arbustos (remoción mecánica, control químico/ con 2,4-D y fuego prescrito) combinados con fertilización de NPK para reducir la cobertura del arbusto y promover el crecimiento de la vegetación herbácea apetecible. El control químico fue el tratamiento más efectivo, después de dos años de tratamiento la cobertura de “Prickly burnet” estaba reducida a un 40% de la cobertura inicial. La remoción mecánica mantuvo la cobertura del arbusto en un 60% del nivel inicial, mientras que el efecto del fuego no fue detectable después de dos años. La vegetación herbácea anual y perenne se correlaciono negativamente con la cobertura del arbusto. La fertilización no tuvo efecto en la cobertura de los componentes vegetativos, pero incremento la biomasa de los parches de vegetación herbácea, el aumento de biomasa varió de 25 a 250% dependiendo del tratamiento. Nuestros resultados demuestran la capacidad de recuperación excepcionalmente alta del "Prickly burnet" al disturbio o intento de erradicación, convirtiendo en inefectivas a la mayoría de las opciones de manejo evaluadas. El mejoramiento efectivo del pastizal dominado por “Prickly burnet” requiere , muy probablemente, de un tratamiento combinado incluyendo la remoción de arbustos maduros, suprimiendo su recuperación y estimulando el componente de zacates competitivos.

The relationships between woody and herbaceous vegetation are of foremost significance for free-ranging livestock. In most cases, woody vegetation provides a limited contribution to the livestock diet whereas it may dominate the space available for forage plants. Concomitantly, herbaceous vegetation, the most significant diet component for herbivores, may be replaced by woody species.

Human intervention such as shrub removal, aimed at decreasing woody cover while increasing herbaceous yield, began in the Mediterranean region in historic times (Naveh and Dan 1973) and has continued ever since (Passera et al. 1992).

Continuous severe exploitation of the evergreen dense *maquis*, which prevails in the Mediterranean Basin, caused its degradation to a dwarf shrub formation known in Israel as *batha* and in Greece as *phrygana*. The dominant species in these communities in the east Mediterranean is the thorny and unpalatable dwarf shrub prickly burnet (*Sarcopoterium spinosum* (L.) Spach.). Prickly burnet is a common invader of abandoned cropland (Litav and Orshan 1971). According to pollen records, prickly burnet was present in northern Israel as early as the 3rd century A.D. (Baruch 1986). In many cases, the prickly burnet community comprises a long-standing, sustainable pioneering stage (Zohary 1962).

Range improvement within the context of Mediterranean ecosystems primarily means preventing woody vegetation from replacing the herbaceous vegetation - the main source of palatable forage. Such management, in fact, opposes the natural trend of succession in most Mediterranean ecosystems and, therefore, requires active intervention. As a result, Mediterranean grass-

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lands are, in a sense, a 'successional anticlimax'; the term itself is something of an oxymoron (Seligman 1996).

The working hypothesis in this study was that under existing conditions, management treatments can establish a new balance between dwarf shrubs and herbaceous vegetation. Specifically, we wanted to determine the feasibility of improving chalk rangelands through shrub removal by mechanical means, selective herbicide application, or controlled burning while enhancing growth of herbaceous vegetation by fertilizer application. The assumption behind the research was that the combined effect of shrub control and nutrient amelioration can create a stable grassland community.

Materials and Methods

Experimental Site

The experimental site is located in northern Israel, in the hills of the lower Galilee, 15 km east of Haifa and the Mediterranean coast (32°43'N 35°06'E). The site is situated on the upper part of a 5% south-facing slope, at 100 m above sea level. The climate is semi- humid Mediterranean; mean annual rainfall is 600 mm (ranging from 400 to 700), occurring mostly during winter (90% in December–February). Average annual temperature is 19° C (Average December temp. is 10° C, August 28° C). The bedrock is Eocenian chalk, covered by dark grey Rendzina (Haploxerolls) soil (Dan et al. 1962).

Vegetation is dominated by *S. Spinosum* (L.) Spach, with other woody species and vines, remnants of vallonea oak (*Quercus ithaburensis* Decaisne) savanna that covered the region in historical times. Dominant perennial grasses at the site are *Dactylis glomerata* L. and *Andropogon distachyus*. L. Among annual grasses, *Avena sterilis* is the most common.

Experimental Design

Forty, 5 x 5 m plots, with a separating buffer zone of 0.5 m, were established in a relatively homogeneous area. The experimental site was fenced against human or livestock disturbance in autumn of 1989. The experimental design included 2 levels, the first consisting of 4 shrub removal treatments: 1) control; 2) shrub removal by manual means with minimal soil disturbance; 3) herbicide spraying with 5 liter ha^{-1} of 2,4-D applied as a 2% solution in 50 liter of water; and 4) controlled burning of the shrub canopies.

Shrub removal was implemented during autumn (November 1989). 'Shrub removal' involved hoeing-off the aboveground parts of the *S. spinosum* and removal of the material from the experimental site. Herbicide spraying was implemented in mid- winter of the first year (January 1990). Herbicide was applied from a back sprayer as a foliage wetting spray covering all of the plant green parts until the spray dripped off. The herbicide, 2,4-D, effectively kills mature prickly burnet shrubs and is frequently used for dwarf shrub control on rangelands in Israel (e.g. Seligman and Katzir 1965, Gutman et al. 1990). Controlled burning was very localized, conducted by spraying each shrub individually with fuel from a back sprayer and igniting it. Under these conditions, fire had very little impact on the surrounding vegetation.

The second experimental level was application of 50 kg ha^{-1} of a composite fertilizer (20N-20P-20K: 10% urea + 6% NO3 + 4% NH4 + 20% P_2O_5 + 20% K_2O, a product of Haifa Chemicals). Ten liters of fertilizer solution were sprayed evenly on each treated plot. Fertilizer was applied in winter, once each year, after the first effective rainfall.

Five replications of each of the 4 shrub removal treatments were randomly assigned to 'no fertilization' treatment; 5 additional replications of the same treatments were also randomly selected and assigned to fertilization treatment.

Vegetation Monitoring

Four permanent transects (totalling 20 m) were established, at equal intervals, across each experimental plot. Presence or absence of vegetation components (*S. spinosum*, perennial grasses and annual grasses) was recorded every 10 cm along the transect (200 points/plot) using a wirepin. The ratio between number of hits per life-form (Z) and total number of points (Z/200 * 100), served as a measure of aerial cover (%). The first vegetation monitoring was conducted before treatment application (autumn 1989), and then in the following 2 spring seasons (1991, 1992).

Yield (biomass) of herbaceous vegetation (including annual and perennial, grasses and forbs together) was determined each year in the peak growing season (early April). Ten, 25 x 25 cm quadrats were distributed at random in each plot, and all herbaceous vegetation within each quadrat was clipped. Samples were dried at 80° C for 3 days and then weighed. Herbage yield (g m^{-2}) from each plot was calculated as the average of the samples.

Data Analysis

Data were analyzed by SAS-PC software (SAS 1988). Treatment and interaction effects were tested by Two-Way Analysis of Variance (ANOVA). Data on plant cover for this procedure were arcsin of square root transformed. If there was no

Table 1. Two-Way ANOVA of the effect of shrub removal and fertilization and their interaction on herbaceous biomass and relative abundance of vegetative components.

		Model		Shrub Removal (ShR)		Fertilization (F)		(ShR) * (F)	
	(F (df = 7)	P	R2	F (df = 3)	P	F (df = 3)	P	F (Df =3)	P
1991									
Herbage Biomass	2.49	0.366	0.35	3.98	0.0162	68.63	0.0582	0.55	0.6535
SRPT Cover	29.72	0.0001	0.87	65.85	0.0001	0.6555	0.2	3.43	0.0286
PRGR Cover	7.75	0.0001	0.63	16.46	0.0001	0.31	0.5819	1.53	0.2253
ANGR Cover	1.68	0.1494	0.27	0.78	0.5165	0.61	0.4405	2.94	0.0479
1992									
Herbage Biomass	7.34	0.0001	0.62	6.6	0.013	24.44	0.0001	2.38	0.0878
SRPT Cover	8.84	0.0001	0.66	17.46	0.0001	0.89	0.3512	2.88	0.0509
PRGR Cover	4.85	0.008	0.51	10.18	0.0001	0.01	0.9301	1.14	0.3496
ANGR Cover	1.84	0.1137	0.29	3.18	0.0373	0.61	0.4402	0.91	0.4461

SRPT = Sarcopoterium spinosum
PRGR = Perennial grasses
ANGR = Annual grasses

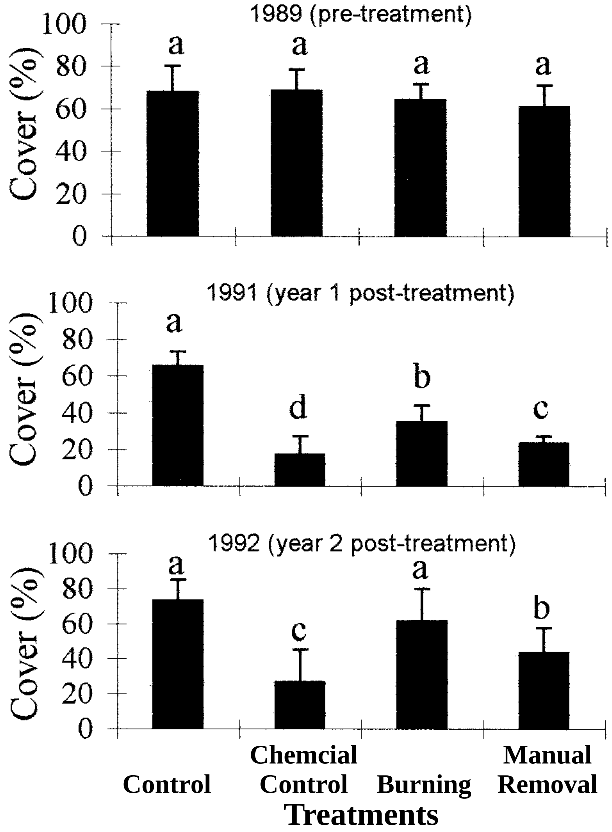

Fig. 1. Treatment means (± SE) for prickly burnet (*Sarcopoterium spinosum*) cover (%). All treatment means within the same year followed by a different letter are statistically different at the 5% level.

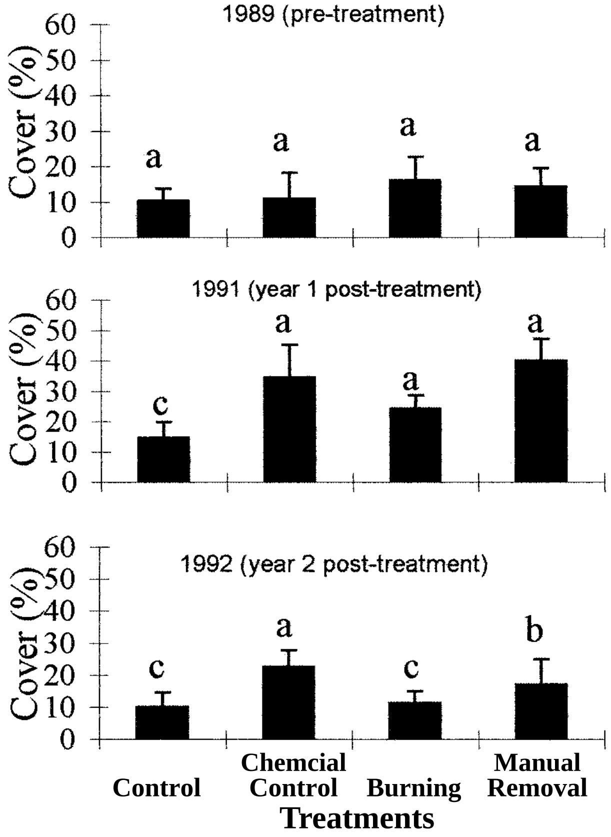

Fig. 2. Treatment means (± SE) for the cover of perennial grasses. All treatment means within the same year followed by a different letter are statistically different at the 5% level.

effect of fertilization treatments, vegetation data of fertilized and unfertilized plots of each shrub removal treatment were combined, thus increasing sample size. All differences discussed are statistically significant at the 5% level unless otherwise indicated.

Effects of shrub removal treatments and fertilization on cover of all vegetation components were also analyzed by canonical analysis (CANOCO). This program was developed specially to present multiple species' response to environmental factors (Ter Braak and Prentice 1990). Canonical Correspondence Analysis (CCA) was applied to arcsin transformed percentage cover (%+1) data using the various treatments as environmental variables. The Monte Carlo test was used to test the hypothesis that distribution of vegetation components among different treatments along the first ordination axis was random.

Results and Discussion

All vegetation parameters, except annual grasses, were increased by both shrub removal and fertilization (Table 1). This outcome combines the impact of shrub removal on both biomass and cover, and the fertilization effect on biomass. The interaction of shrub removal X fertilization was significant on *S. spinosum* in both years and on annual grasses in 1992. The fact there was no effect of fertilization on plant cover allowed us to combine all data (with and without fertilization) for further analyses.

There were no differences in prickly burnet cover among plots prior to treatments (Fig. 1. 1989). Immediately after the manual removal and burning treatment (January 1990), prickly burnet cover was nearly zero. One year post-treatment (spring 1991), prickly burnet cover in the control plots had not changed (65.3%), whereas burning, manual removal, and herbicide treatments, reduced its cover to 34.9%, 23.4% and 17.2%, respectively. Two years after treatment (spring 1992) cover in burned plots had already recovered, almost reaching the level of the control plots (61.2%). In manual-removal plots, prickly burnet cover increased to 43.3%, whereas in herbicide plots, there was a relatively small change in cover, increasing only to 25.7%.

There were no differences in perennial grass cover among plots prior to treatment (Fig. 2. 1989). Cover of perennial grasses in 1991, in all treated plots, increased when compared with untreated control plots (14.5%). In manual-removal, herbicide and burned plots, perennial grass cover was 40%, 34.5% and 24.2%, respectively. One year later (spring 1992) there was no difference in cover of perennial grasses between burned and control plots (~10%). However, in manual-removal and herbicide treatments, perennial grass cover was still greater than in the control (Fig. 2).

In contrast to prickly burnet and perennial grass cover, annual grass cover was much lower and not homogeneous among

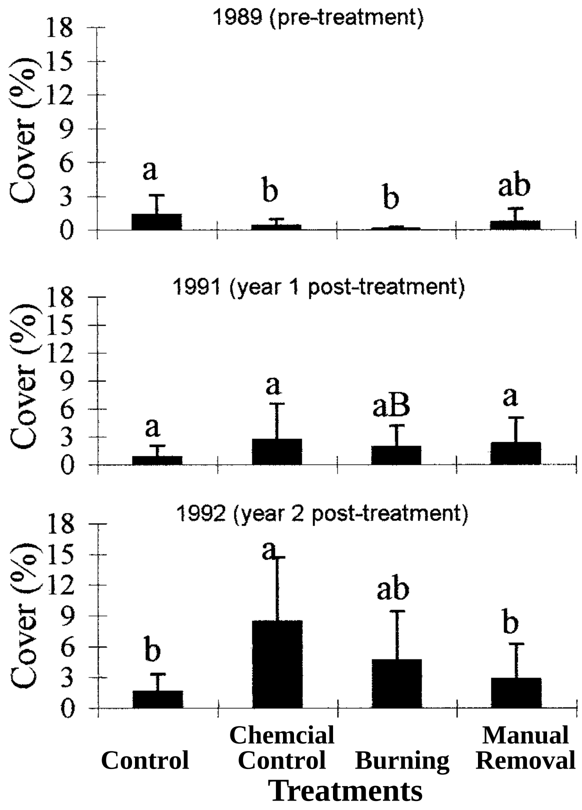

Fig. 3. Treatment means (± SE) for the cover of annual vegetation. All treatment means within the same year followed by a different letter are statistically different at the 5% level.

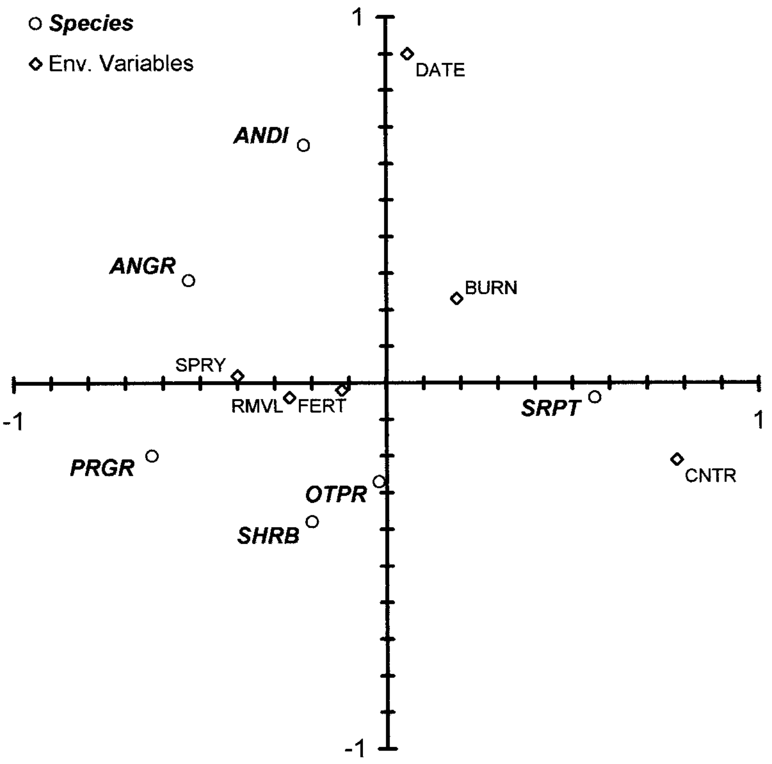

Fig. 4. An ordination plot of the treatment effects on the cover of all vegetation components.

the experimental plots prior to treatment (Fig. 3). Cover of annuals was greater in control plots probably because of the spatial variability and low absolute values of cover in undisturbed situation. One year after treatment, cover of annuals in treated plots was somewhat greater ($p \cong 0.52$) than that of the control. After 2 years this trend was maintained and even became more pronounced. In the burned, manual-removal and herbicide treated, cover was 4.6%, 2.8%, and 8.4%, respectively compared to 1.6% in the control plots.

Some treatments—herbicide (SPRY), manual-removal (RMVL) and fertilization (FERT)—affected cover of *S. spinosum* negatively and therefore are located far from the control (CNTR) along the horizontal axis of the canonical ordination plot (Fig. 4). The burning treatment (BURN), on the other hand, is relatively close to the control. Time since treatment (DATE) also had a limited impact on the vegetation. The same treatments, however, increased annual and perennial herbaceous species (annual grasses and perennial grasses). The Eigen value of the first axis is 0.03; a Monte Carlo test showed that distribution of species along the first axis of the ordination plot was not random.

Total herbaceous biomass in 1991 was increased by shrub removal treatments, but only partly by fertilization ($p \cong 0.06$); in 1992 it was increased by both removal and fertilization (Table 1). In 1991 herbicide and removal treatments produced higher biomass yields than the control, but there was no fertilization effect (Fig. 5). In 1992 fertilization caused an increase in herbaceous biomass in all experimental plots as compared to either unfertilized (except in herbicide treatment) or untreated plots (Fig. 5).

Productivity of Mediterranean rangelands is limited by a relatively high cover of woody vegetation (Seligman 1996) as well as by a low level of essential minerals (N or P) in the soil (Osman et al. 1991, Henkin et al. 1996). This study examined the effects of manipulating these 2 driving factors (shrub cover and soil mineral content) on the structure and productivity of the herbaceous vegetation community growing on chalky habitats.

All shrub removal treatments applied in this study generated a drastic reduction of prickly burnet cover in the experimental plots, immediately after treatment. However, treatment-related differences were recorded in recovery rate of prickly burnet. Spraying with 2-4D was the most efficient treatment and 2 years after treatment, prickly burnet cover reached only

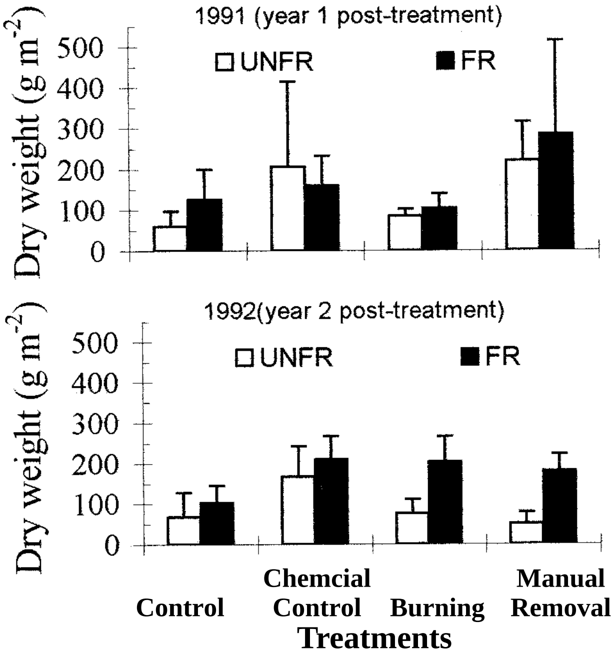

Fig. 5. The effect of fertilization on the biomass (means ± SE) of herbaceous vegetation for control, herbicide, burning and shrub removal treatments.

40% of the initial value. Manual removal was moderately effective, reaching 60% of the original value after 2 years. Controlled burning decreased shrub cover for a very limited period of time, but prickly burnet regained almost all its original cover within 2 years from burning. In Greece prickly burnet returned to pre-burning biomass level within 4.5–7.5 years (Papanastasis 1980). In Israel, under different environmental conditions (terra-rossa soil on hard limestone), prickly burnet cover increased to its original cover after burning at a slower rate (less than 6 years - Henkin et al. 1998).

Aggressive regrowth of prickly burnet is mostly a result of intensive resprouting from underground adventive basal buds (Litav and Orshan 1971, Papanastasis 1980). However, its rapid recovery after burning is, most certainly, a consequence of a combined effect of the intensive resprouting and a fire-stimulated germination (Arianoutsou-Faraggitaki 1984). Germination rate of prickly burnet was 10 times higher on burned sites than on unburned plots (Arianoutsou and Margaris 1981).

The herbicide treatment had a lethal effect on prickly burnet shrubs and inhibited resprouting in comparison to the control. It may also have reduced germination by the shading effect of the dead canopy on light-controlled germination (Litav et al. 1963). In a similar experiment, under different environmental conditions, herbicides reduced prickly burnet cover drastically and after 6 years it reached not more than one-third of its original cover (Henkin et al. 1998).

Fertilization had no effect on regrowth of prickly burnet, indicating that mineral nutrition was not a limiting factor for shrub development in the studied ecosystem. This seems to contradict statements that the Mediterranean ecosystem is limited by nutrients (Kruger 1987). However, fertilizer application did increase herbage yield, especially in the second year. The Eocene rendzina is much richer in available nutrients than the more widespread hard limestone habitats.

Prickly burnet removal made available new sites and resources for other vegetation components. Consequently, abundance (cover) of perennial grasses increased when prickly burnet cover decreased. The most effective treatments in removing prickly burnet (manual removal and herbicide spraying) also stimulated most strongly the growth of perennial grasses. Fast recovery of prickly burnet from removal, reduced the relative increase of perennial grasses (1992 vs 1991).

Absolute cover of annuals in prickly burnet dwarf shrub formation is very low, probably due to competition by taller plant life-forms (shrubs and perennial grasses) under stressful conditions (low levels of soil moisture). Annuals did not respond as quickly as perennial grasses to removal of prickly burnet, and the main increase in their cover was during the second year. This observation is related, most probably, to seed-bank limitations (Looney and Gibson 1995), thus explaining the time lag of 1 year before annuals became more abundant. Here too, a higher abundance of annuals was facilitated by a lower shrub cover as a result of herbicide spraying.

Our observations do not support the hypothesis that the applied treatments can easily change the community structure and create a new balance among vegetation components. The most prominent conclusion of this study is that, despite drastic interventions (fire, manual-removal and herbicide treatments), the prickly burnet community recovers quickly and returns to its original structure within a few years. In other words, it creates a very resilient formation (Fox and Fox 1988). In particular this is the case on fertile, soft chalk habitats, where prickly burnet establishes easily and rapidly from seeds and grows vigorously. On terra-rossa overlying hard limestone, growth of prickly burnet is much less vigorous, and recovery after burning is slower (Henkin et al. 1998).

Our results support the notion that the most efficient option for suppressing encroaching shrubs is to combine treatments (Scifres 1987), some of them drastic. Such a combination should include a tool to remove mature shrubs (e.g. mechanical treatment or fire), a suppressing tool to obviate recovery of removed shrubs (selective herbicide spraying), and a grass-stimulating tool (fertilization or sludge application) that will make the herbaceous stand denser, thus helping it to compete with prickly burnet seedlings for resources (light, water). To maximize the outcome of such combined management practice, shrub removal should be conducted in autumn (before the rains; Papanastasis 1980), selective spraying (anti-dicot)—in the following late spring or summer, and fertilization—after the first rains of the second year. Nevertheless, the cost of such a combined shrub control procedure may be excessive where rangelands are degraded by heavy grazing and/or erosion.

Our results also explain why grasslands are not common in the east Mediterranean (Seligman 1996) and why range improvement in this environment is expensive and frustrating. However, rapid shrub encroachment and an increasing fire hazard make attempts to control shrub cover in the Mediterranean ecosystems an important and relevant management challenge (Perevolotsky and Seligman 1998).

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Hydrologic responses of a montane riparian ecosystem following cattle use

M. FLENNIKEN, R.R. MCELDOWNEY, W.C. LEININGER, G.W. FRASIER, AND M.J. TRLICA

Authors are resource specialist, Larimer County Parks and Open Lands Department, 1800 S. County Rd. 31, Loveland, Colo. 80537; riparian/wetland ecologist, Science Applications International Corporation, 8100 Shaffer Parkway, Suite 100, Littleton, Colo. 80127, professor, Rangeland Ecosystem Science Department, Colorado State University, Fort Collins, Colo. 80523; research hydraulic engineer, USDA, Agricultural Research Service, Fort Collins, Colo. 80526; and professor, Rangeland Ecosystem Science Department, Colorado State University, Fort Collins, Colo. 80523. At the time of the research, both the first and second authors were graduate research assistants, Rangeland Ecosystem Science Department, Colorado State University, Fort Collins, Colo. 80523.

Abstract

Riparian areas link streams with their terrestrial catchments and decrease water pollution by trapping sediments from upland sources before they reach streams or lakes. Livestock grazing in riparian areas is a controversial practice. If not properly managed, cattle can cause degradation to both the riparian zone and adjacent water body. Vegetative, soil microtopographical, microchannel and hydrograph parameters were measured in a montane riparian community in northern Colorado to quantify the effects of cattle on overland flow and runoff characteristics. Treatments were cattle grazing plus trampling, cattle trampling, mowing, and a control. Water was applied to plots (3 m x 10 m) at a rate of 100 mm hr^{-1} using a rainfall simulator. Concurrently, overland flow was introduced at the upper end of the plots at an equivalent rate of 25 mm hr^{-1}. A high intensity-short duration grazing treatment was used for the cattle-treated plots. Reduction in vegetation stem density and aboveground biomass by cattle decreased microchannel sinuosity and drainage density. Cattle-treated plots had greater flow velocities and depths in microchannels compared with mowed and control plots. Reduced stem density and aboveground biomass by grazing left fewer obstacles to divert flows, which decreased microchannel sinuosity and drainage density. Flows were concentrated into fewer microchannels with deeper flows. Microchannel characteristics were not significant factors affecting total runoff. Stem density and rainfall intensity were the most important factors in predicting runoff characteristics and total runoff. Results from this study have improved our understanding of flow and runoff processes following cattle use of a riparian ecosystem.

Key Words: runoff, stem density, microchannels, sinuosity, drainage density, rainfall simulation

Resumen

Las áreas ribereñas vinculan las corrientes con sus áreas de captación terrestres y disminuyen la contaminación del agua atrapando los sedimentos provenientes de terrenos altos antes de que lleguen a las corrientes o lagos. El apacentamiento de ganado en áreas ribereñas es una practica controversial. Si no es manejada apropiadamente, el ganado puede ocasionar la degradación tanto del área riberña como la del cuerpo de agua adyacente. En una comunidad ribereña montana del norte de Colorado se midieron parámetros vegetativos, microtopográficos del suelo, de microcanales e hidrográficos para cuantificar los efectos del ganado en el flujo superficial y las características del escurrimiento. Los tratamientos fueron: apacentamiento de ganado mas pisoteo, pisoteo de ganado, siega y un control. El agua se aplicó a las parcelas (3 m x 10 m) a una tasa de 100 mm hr^{-1} utilizando un simulador de lluvia. Concurrentemente, el flujo superficial se introdujo en el extremo superior de las parcelas a una tasa equivalente de 25 mm hr^{-1}. En las parcelas tratadas con ganado se utilizó un sistema de apacentamiento de alta intensidad-corta duración. La reducción en la densidad de tallos y biomasa aérea causada por el ganado disminuyo la sinuosidad de los microcanales y la densidad de drenaje. Las parcelas tratadas con ganado tuvieron velocidades de flujo mas altas y profundas en los microcanales que las obtenidas en las parcelas segadas y control. Una densidad de tallos y biomasa aérea reducidas por el ganado dejan pocos obstáculos para desviar flujos, lo cual disminuye la sinuosidad de los microcanales y la densidad de drenaje. Los flujos se concentraron en unos pocos microcanales con flujos profundos. Las características de los microcanales no fueron factores significativas que afectaran el escurrimiento total. La densidad de tallos y la intensidad de la lluvia fueron los factores mas importantes para predecir las características del escurrimiento y el escurrimiento total. Los resultados de este estudio han mejorado nuestro entendimiento de los procesos de flujo y escurrimiento después de que el ganado uso los ecosistemas ribereños.

Suspended sediments can increase water turbidity, transport nutrients and pollutants attached to soil particles, and eventually be deposited in streambeds or lakebeds. Vegetation filter strips (VFS), or bands of planted or indigenous vegetation located between sediment sources and streams, can reduce suspended sediment from overland runoff. The efficiency of VFS to filter sediment depends on surface microtopography, vegetation cover, density and type, slope, and length of the buffer strip (Landry and Thurow 1997). Riparian zones link streams with their terrestrial catchments and serve as natural VFS by trapping sediments from upland sources before they reach streams (Osborne and Kovacic 1993, Daniels and Gilliam 1996, Hairsine 1996). Many models of VFS sediment filtration assume shallow sheet flow (Dillaha

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1989). However, overland flow in grasslands generally does not travel as a uniform sheet, but is concentrated into small channels (microchannels) (Dillaha 1989). Microchannels, for the purpose of this study, were defined as flow paths among the vegetation clumps, normally up to 10–20 cm wide and carrying water 1–2 cm deep. In a montane riparian ecosystem, Fernald (1997) evaluated runoff as a factor of vegetation type and microchannel density and documented 1 to 3 primary microchannels in each study plot (3 m wide x 10 m long). The density and sinuosity of microchannels may be important determinants of riparian surface hydrology, thus affecting surface runoff rates and sediment delivery to streams.

Livestock grazing effects on infiltration, runoff, and sediment production in uplands have been well studied (Packer 1953, Lusby 1970, Bohn and Buckhouse 1985, Thurow et al. 1986). Grazing intensity, grazing system, timing of grazing, level of defoliation, and amount of trampling have all been shown to affect infiltration, runoff, and sediment yield (Packer 1953, Bohn and Buckhouse 1985, Thurow et al. 1986). Effects of livestock grazing on riparian communities typically involve alteration through soil compaction (Kauffman et al. 1983, Bohn and Buckhouse 1985), defoliation, and physical damage to vegetation (Roath and Krueger 1982, Schulz and Leininger 1990). However, information on specific livestock impacts to a riparian landscape and consequential effects on riparian hydrologic processes is limited. While the results of improper riparian grazing practices on infiltration and runoff have been described elsewhere, little is known about which aspect of livestock use (hoof action or canopy removal) has the greatest effect on riparian surface hydrology.

It was hypothesized that cattle would change runoff and overland flow characteristics by physically affecting both soil and vegetation properties. The objective of this study was to quantify the effects of vegetation mowing, cattle trampling, and cattle grazing plus trampling on soil and vegetation and how these parameters in turn affected runoff and overland flow characteristics through the riparian zone.

Methods

Site Description

Research was conducted in a riparian meadow adjacent to Sheep Creek in the Roosevelt National Forest, about 80 km northwest of Fort Collins, Colo., at an elevation of 2,500 m (Lat 40° 59.725', Long 105° 43.265'). The soils are a sandy loam to clay loam texture stratified with thin layers of sand or clay of the Fluvaquents series (USDA 1980). In places the water table is less than 30 cm at some time during the spring and summer. There was a heavy organic O horizon as much as 20 cm thick in the study site. Soil texture of the surface 7 cm at the study sites was 36% sand, 36% silt, and 26% clay (clay loam texture). Some mottling was evident, indicating recurrent seasonal soil saturation. The south-facing slopes of the experimental plots ranged from 3 to 5%.

Vegetation at the site was dominated by Kentucky bluegrass (*Poa pratensis* L.), small-wing sedge (*Carex microptera* Mack.), water sedge (*Carex aquatilis* Wahl.), tufted hairgrass (*Deschampsia caespitosa* (L.) Beauv.), Baltic rush (*Juncus balticus* Willd.), western yarrow (*Achillea lanulosa* L.), and marsh marigold (*Caltha leptosepala* DC.).

Plot Installation and Rainfall Simulator

Sixteen, 3 × 10 m plots (25.7 to 28.8 m^2) were used to evaluate overland flow and runoff in the montane riparian filter strip. Plots were placed perpendicular to Sheep Creek. Plots were paired (3 m apart) for rainfall simulations where a ‘Swanson’ large rotating boom rainfall simulator (Swanson 1965) was used to apply water to evaluate runoff and overland flow (Laflen et al. 1991, Frasier et al 1998b). Overland flow was contained within 0.15 × 3 m steel borders × 6 cm driven into the ground along the upper edge and 2 sides of each plot (Pearce et al. 1998). A headwall, flush with the ground surface, was established along the bottom edge of each plot. Steel gutters that lined the headwall collected surface runoff and channeled it through a pre-calibrated flume.

Treatments

One of 4 treatments was applied to each plot. Treatments included:

1. Grazed plus trampled: To simulate a heavy stocking rate, three, 320-kg heifers were fenced on plots for 8 hours, coinciding with peak feeding times (1600–2000 and 0400–0800 hours).
2. Trampled: Three, 320-kg heifers were fitted with nylon mesh muzzles and fenced on plots for 8 hours (1600–2000 and 0400–0800 hours).
3. Mowed: Plots were mowed with a lawnmower to a 10 cm stubble height and clippings were removed.
4. Control: Natural vegetation height; no treatment administered.

Feces remained on the cattle-treated plots.

Plot Characterization

Microtopography

Microtopography was measured using a 100-point (10 x 9.6 cm grid) elevation table (0.6 x 2 m dimension) positioned lengthwise across the center of each plot. Elevation table measurements were made before and after treatments, as well as after the final rainfall simulation. Pin height (mm) above the horizontal table surface was measured with a digital caliper. Microtopography was charcterized by the Revised Universal Soil Loss Equation (RUSLE) method using the maximum range in pin elevations (Renard et al. 1997).

Soil

Three soil bulk density samples for 0–5 and 5–10 cm depths were randomly taken from each plot with a 7.5 cm diameter soil core sampler before treatment. Soil plugs, taken from directly outside of the plots, were used to refill the holes. Bulk density was resampled on the grazed and trampled plots following treatment. The soil cores were composited by plot and depth class. Three, 50 mg, air-dried subsamples per plot were later combusted at 600° C for 4 hours to determine organic matter (OM) content. Gravimetric soil moisture in the top 10 cm of soil was determined with 3 samples taken from each plot just prior to pre-conditioning, and again before the post-treatment rainfall simulation. Each soil moisture sample was weighed, dried in a microwave oven in 5 min increments until less than a 0.5 g change in weight occurred, and then reweighed.

Vegetation

Vegetation density (stems m^{-2}) was measured at ground level and categorized by class (*i.e.*, grasses, forbs, sedges, and Baltic rush) using a 10 x 10 cm quadrat. Before all treatments and again after the grazed and trampled treatments, the number of stems in 10 randomly placed quadrats within the lower 2/3 of each plot was recorded. Stem width at ground level was measured at 10 random locations within the lower 2/3 of each plot (*i.e.*, 10 stems of each vegetation class were measured per plot).

Vegetation was clipped to ground level in a 1/8 m^2 circular plot and bagged to estimate aboveground biomass. Five biomass samples were randomly taken in each plot before and after treatment. The trampled treatment was only sampled before treatment. Samples were dried in a forced draft oven for 72 hours at 50° C before weighing.

Microchannels

Microchannel sinuosity was indexed for each plot as the ratio of channel length to the straight line distance between 2 fixed points approximately 1 m apart (George and Sidle 1995). The closer the sinuosity values are to 1, the straighter the flow paths. Microchannel sinuosity was measured within 10 random grid sections per plot. Drainage density (m m^{-2}) was calculated by measuring the total length of microchannels within a plot divided by the plot area (adapted from Schumm and Hadley 1959). Flow depths in microchannels were measured during equilibrium runoff with a ruler to the nearest mm at 6 random locations, both downslope and cross-slope within each plot during the simulation run.

Rainfall Simulations

Two rainfall simulation runs, about 24 hours apart, were made on each plot pair; one before (pre-treatment) and one after (post-treatment) treatments were applied.

Water was applied to the plots at an approximate rate of 100 mm $hour^{-1}$ for a total run time of about 100 min. This rate was equivalent to approximately double that of a 100 year-1 hour rainstorm event and was chosen based on studies by Pearce et al. (1998). The rate of application was also selected to insure there would be sufficient amount of water to exceed the infiltration rate. Total quantities of water applied were measured with 6 rain gages placed within each plot. Actual simulation intensities were recorded for each plot pair with an 8 cm diameter volumetric raingage equipped with a bubble gage pressure transducer. Concurrent with rainfall simulation, overland flow was simulated by spraying water onto a 3.0 x 0.6 m tilted input tray at the top of each plot at the equivalent rate over the entire plot of 25 mm $hour^{-1}$. Runoff was measured at the outlet of each plot with a pre-calibrated critical depth flume and data were recorded by bubble gage pressure transducer recorders in 1 min intervals.

Pre-treatment Rainfall Simulation

Plots were preconditioned 24 hours before treatments using the rainfall simulator. The preconditioning was done to minimize soil moisture variability among plots and to increase the soil's vulnerability to compaction (Warren et al. 1986). A dye tracer was applied as a line source at 2 locations (3 and 6 m downslope from the top of plot) across each plot to allow identification of the water front advancement and flow paths down the plots (Fernald 1997). All runoff events were recorded and timed on video to allow re-examination of channel locations at a later date and to determine the peak channel velocity of the water movement downslope. Strings stretched across each plot on a 50 x 50 cm grid were used to estimate water velocity through the microchannels as the dye moved downslope. Immediately after the preconditioning event, the primary microchannels as delineated by the dye tracer were spray painted and photographed.

Post-Treatment Rainfall Simulation

Following treatments, rainfall was simulated again over the paired plots. Concurrent with rainfall application, overland flow was again introduced at the top of the plot at the equivalent rate of 25 mm $hour^{-1}$ over the entire plot. During the rainfall simulation, a dye tracer was again applied as a line source across the plots at the same locations and flow rates and paths were recorded on video and timed. Immediately after the simulation, the primary microchannels were again delineated with spray paint and photographed.

Runoff Hydrograph

A runoff hydrograph is a graphical representation of a runoff event showing the change in runoff rate through time. Hydrographs can be divided into their constituent parts for analysis of treatment effects (Simanton et al. 1991, Frasier et al. 1998a, 1998b). Hydrograph components analyzed in this study included time to runoff initiation, slope of the rising limb, time to equilibrium, equilibrium runoff, slope of the falling limb, and total runoff.

Breakpoints between hydrograph segments were estimated using an iterative least squares regression process developed by Brakensiek et al. (1979) for analysis of precipitation data. Regression coefficients from rising limb and falling limb trend lines were considered the slopes of these hydrograph components. Time to equilibrium runoff was determined when a constant rate of flow occurred for 2 consecutive recorder readings (4 min).

Weather conditions and slight differences among spray nozzles caused varying application rates, even among paired simulation plots. To compensate for this, accumulated runoff values were normalized in 1 min intervals into percentages [(runoff rate/total application rate) x (100)] (Frasier et al. 1998b). Accumulated runoff after 60 min of simulation was also evaluated for treatment effects. The 60 min time frame was selected because it was common to all simulations.

Experimental Design

A randomized complete block (RCB) design was used for this experiment. There were 4 treatments (grazed plus trampled, trampled, mowed, and control) and 4 blocks. Soil and vegetation responses were included as covariates to explore their relationships with treatment effects. Multiple regression models were constructed for microchannel sinuosity, drainage density, flow depths, accumulated runoff, time to runoff initiation, slope of the rising limb, time to equilibrium, equilibrium runoff, and slope of the falling limb using forward and stepwise selection processes. The independent variables for these models included: slope, plot area, stem density by vegetation class, overall stem density, sinuosity, drainage density, flow depths, rainfall intensity, spraybar intensity, aboveground biomass, soil organic matter, soil bulk density, soil moisture, surface roughness, ground cover, stem basal widths, and pre-treatment values for each variable. Unless stated otherwise, significance was determined at $P \leq 0.10$. Data were analyzed using SAS® for Windows® (SAS® 1996).

Results and Discussion

Variables not affected by cattle treatments

Microtopography

There were no significant differences among treatments for random surface roughness using the RUSLE method (Flenniken 1999, McEldowney 1999). The large amount of organic matter on the plots may have acted like a sponge and was not altered by the treatments. The connectivity of microtopography may be a more important characteristic in riparian hydrology than variations in surface roughness (Fernald 1997, Frasier et al. 1998b). The connectivity of microtopographical soil surface features may directly influence flows through microchannels and subsequent runoff rates.

Soil moisture and organic matter

Soil moisture and soil organic matter estimates for the top 10 cm of soil were

Table 1. Summary data for selected variables for each of the 4 treatments applied to a montane riparian community.

	TREATMENT			
Parameter	Control	Mowed	Trampled	Grazed
POST-TREATMENT				
Plot area (m^2)	28.8b	27.3ab	26.8a	27.4ab
Slope (%)	3.8a	3.6a	4.2a	3.8a
Rainfall intensity (mm hour^{-1})	102b	89a	89a	102b
Spraybar runon intensity (mm hour^{-1})	25.7a	26.6a	27.4a	27.8a
Soil moisture (%)	36a	36a	36a	36a
Soil organic matter 0-5 cm (%)	19.3a	20.6a	19.5a	22.4a
Soil organic matter 0-10 cm (%)	10.1a	10.8a	12.2a	11.3a
Bulk density 0-5 cm (g cm^{-3})	0.6a	0.6a	0.7a	0.6a
Bulk density 0-10 cm (g cm^{-3})	0.9a	0.9a	0.9a	0.9a
Stem density (# stems m^{-2})	5275bc	5525c	4650b	3300a
Litter ground cover (%)	63a	65a	61a	62a
Aboveground biomass (kg ha^{-1})	2330b	1725a	*	924a
Microchannel sinuosity	1.24c	1.17b	1.04a	1.04a
Drainage density (m m^{-2})	2.1b	2.4b	1.7a	1.7a
Flow depth in microchannels (mm)	18a	24ab	26b	32c
Accumulated runoff after 60 min (%)	45.2ab	35.0a	48.8b	67.3c
Time to runoff initiation* (min)	14.3b	22.2c	12.8ab	9.0a
Slope of the rising limb* (%)	8.4a	9.0ab	7.0a	16.6b
Time to equilibrium runoff (min)	20.9b	34.4d	28.3c	15.8a
Slope of the falling limb -	6.7ab	–7.8a	–5.3bc	–5.1c

Different letters following means in a row indicate significance at $p \leq 0.10$. An * indicates missing data.

not different among treatments (Table 1). However, soil moisture did vary by block; lower soil moisture occurred near the upper part of the riparian meadow and increased with proximity to Sheep Creek.

Bulk density

Soil bulk densities for the 0-5 cm and 5-10 cm soil depths were not affected by cattle activity (Table 1) . In the top 5 cm of soil, bulk density ranged from 0.47 to 0.81 g cm^{-3}; while in the 5–10 cm depth class, bulk density ranged from 0.65 to 1.14 g cm^{-3}. The large amount of soil organic matter, the clay loam soil texture, and the large amount of litter cover all may have contributed to mitigating compaction effects by trampling (Abdel-Magid et al. 1987, Wheeler et al. 2002).

Basal Widths

Basal widths did not vary among treatment. However, basal widths among vegetation classes were different, with forbs having the greatest average basal widths (4.7 mm). Basal widths of sedges, grasses, and Baltic rush were not significantly different from each other (2.8, 1.4, and 1.1 mm, respectively). Average values of stem basal widths were similar to widths measured by Fernald (1997) at the site, with the exception of Baltic rush, which he measured to be wider than grasses.

Variables affected by cattle treatments

Aboveground Biomass

Aboveground biomass was 58% less on grazed plots than on control plots (Table 1). There were significant differences in aboveground biomass for the mowed, grazed, and control plots. The decrease in aboveground biomass on grazed compared with control plots represents the amount of vegetation consumed by grazing or removed via cattle trampling. As a result of logistical constraints, the trampled plots were not sampled for aboveground biomass.

Stem Density

There was a 40% decrease in stem density following cattle grazing, as compared to the control (Table 1). The grazed plus trampled treatment had the lowest average stem density, because cattle removed stems both by pulling up stems with grazing and through hoof shear (Kauffman et al. 1983, Abdel-Magid et al. 1987). Stem density for the trampled treatment was higher than that for the grazed treatment, probably because there was only hoof shear and not the grazing component with the trampled treatment. Specifically, forb stem densities were decreased by 50% on both trampled and grazed plus trampled treatment, as compared with the control. Grass stem densities were reduced approximately 40% on grazed plots as compared with control plots.

Stem density was a very important variable that affected microchannel sinuosity, drainage density, flow depth, accumulated runoff, time to runoff, slope of the rising limb of the hydrograph, time to equilibrium runoff, and the slope of the falling limb of the hydrograph (Table 2). The significant reduction in stem density following both types of cattle treatments subsequently impacted microchannel and runoff characteristics.

Microchannel Characteristics

All microchannel characteristics, sinuosity, drainage density, flow depth, and flow velocity, were significantly affected by decreased stem density on cattle-treated plots. However, other variables were also important and will be discussed specifically below. While microchannel characteristics could have potentially affected runoff characteristics, they were not significant in prediction equations. Rather, stem density was a more important predictor variable (Table 2).

Microchannel Sinuosity

Water flowed down the plots in microchannels, though sheetflow occurred between these microchannels for short distances. Similar intermittent sheetflow between flow lines was observed in laboratory experiments by Mosley (1972). There were no differences among plots for pre-treatment sinuosity. Following cattle treatments, however, the microchannels were straightened. There were no differences in microchannel sinuosity between the trampled and grazed plus trampled treatments, indicating that hoof action was primarily responsible for straightening microchannels. The mowed treatment was intermediate in sinuosity to the control treatment and the cattle-treated plots (Table 1).

Multiple regression analysis was used to identify important variables that correlated with and presumably affected post-treatment microchannel sinuosity data. The important independent variables selected by both stepwise and forward regression analyses were forb stem density and grass stem density ($r^2 = 0.78$)(Table 2). Prosser et al. (1995) showed that root stocks and individual submerged stems deflected water flows. Although no other references could be found that related stem density to microchannel sinuosity, aboveground biomass (which is a function of stem density) can serve as a barrier to sediment transport by causing overland flow to move in a slower, more tortuous path (Thurow et al. 1986). Abrahams et al. (1994) reported

Table 2. Prediction equations for various response variables affected by treatments.

Response Variable	Regression Equation	R^2
Microchannel sinuosity	= 0.81 + 0.0002 (forb stem density (stems m^{-2})) + 0.00006 (grass stem density (stems m^{-2}))	0.78
Drainage density (m m^{-2})	= –0.668 + 0.989 (pre-drainage density (m m^{-2})) + 0.0007 (forb stem density (stems m^{-2}))	0.89
Flow depths (mm)	= 41.7 – 0.006 (aboveground biomass (kg ha^{-1})) – 0.009 forb stem density (stems m^{-2}))	0.95
Accumulated runoff (mm hr^{-1})	= 5.24 – 0.0094(stem density^a (stems m^{-2})) + 0.746(rainfall intensity^a (mm h^{-1})) + 0.159(slope(%))(area^c (m^2))	0.75
Time to runoff initiation (min)	= 77.3 –- 0.755 (rainfall intensity^a (mm hr^{-1})) + 0.00225(stem density^a (stems m^{-2}))	0.84
Slope of rising limb (reg. coeff.)	= 19.44 – 0.0032(stem density^a (stems m^{-2})) + 55.73(soil moisture^a (%)) – 26.51(RUSLE surface roughness^b (in))	0.65
Time to equilibrium (min)	= 67.4 – 0.61(rainfall intensity^a (mm hr^{-1})) – 0.0034(stem density^a (stems m^{-2}))	0.59
Slope of falling limb (reg. coeff.)	= –0.832 – 0.24(sedge groundcover^a (%)) – 0.00095(stem density^a (stems m^{-2}))	0.52

Superscripts $^{a, b, c}$ indicate p-value $\leq$ 0.05, 0.10, 0.15 respectively

that 69% of the variability in resistance to overland flow (using the Darcy-Weisbach friction factor (*f*)) was accounted for by basal plant stems and litter cover on an Arizona grassland. With fewer stems to act as barriers to downslope water flow, sinuosity was reduced in their study.

Forb and grass stems may have been influential in directing and concentrating flows. Forbs had the largest stem basal widths of all vegetation classes, possibly making them more influential in directing microchannel flows and were more important if lost through trampling. A reduction in forb and grass stem density in cattle-treated plots resulted in fewer obstacles to divert flows, and microchannel sinuosity was lower.

In studies of geomorphic processes on small-scale channels in Utah, George and Sidle (1995) observed that many of these small channels functioned like gullies in flow dynamics, partly as a result of their low sinuosity. A gully is a relatively deep, vertical-walled channel. It is possible that the low sinuosity for the cattle-treated plots may have resulted in the microchannels more closely resembling gullies rather than channels. If these microchannels behave more like gullies, greater erosive forces on the channel walls and more movement of sediment during overland flow might be expected, rather than flows characteristic of other types of channels. Future studies might involve closer examination of microchannel dimensions.

Drainage Density

There was no difference in drainage density among plots before treatment. This lack of difference allowed for comparison of drainage density between post-treatment cattle plots and pre-treatment control and mowed plots. Cattle-treated plots had lower drainage densities than either mowed or control plots (Table 1). Average drainage density was 19% lower on cattle-treated plots than on control plots, and 26% lower than on mowed plots. Visual examination of plots before and after treatment confirmed this finding (Flenniken 1999).

The prediction equation that best described drainage density following cattle treatments included the independent variables pre-drainage density and forb stem density (Table 2). The model accounted for 89% of the variation in drainage density among treatments, and indicated that pre-treatment drainage density and forb stem density had significant influences on the final measure of drainage density. Obviously, pre-treatment drainage density would be an important determinant of post-treatment drainage density. Since forbs had the greatest stem basal widths of all the measured vegetation classes, their stems acted as barriers in routing water flow. The decrease in forb stem density on cattle-treated plots from hoof shear resulted in fewer barriers for water diversion and may have caused straightening of the microchannel network.

Flow Depths in Microchannels

Post-treatment downslope water flow depths in microchannels were affected by the treatments. Flow depths in microchannels of the grazed plus trampled treatment were the greatest of the 4 treatments; nearly 80% deeper than in the control treatment (Table 1). There were no differences in downslope flow depths between trampled and mowed treatments, or between mowed and control treatments. The high rainfall rate (~100 mm $hour^{-1}$) and overland flow (25 mm $hour^{-1}$) applied to the plots may have overtopped microtopographical elevations.

The prediction equation for post-treatment downslope flow depths in microchannels included the independent variables of aboveground biomass and forb stem density (Table 2). The model accounted for 95% of the variability in flow depths among treatments. A reduction in aboveground biomass and forb stem density from grazing concentrated water into straightened microchannels. Increased runoff and decreased drainage density following cattle treatments also concentrated water into fewer microchannels, resulting in deeper downslope flow depths in the remaining microchannels.

Flow Velocities

No significant differences in flow velocity existed among the 4 treatments. The leading edge microchannel flow velocity was 0.05 m sec^{-1} on cattle-treated plots, and 0.03 m sec^{-1} on the control and mowed plots. A small sample size is partly responsible for these results, as the videotapes only allowed for estimation of a single velocity on each of the treatment plots. In future studies, this problem could be alleviated by direct measurement of flow velocities in the field utilizing a flow meter or similar method.

Runoff characteristics

On first assessment, it was anticipated that changes in soil characteristics (soil moisture, bulk density, and infiltration rate) would greatly influence runoff characteristics. However, it was not a soil phenomenon but rather changes in surface phenomenon of both vegetation and microchannel characteristics that most significantly influenced runoff.

Accumulated Runoff

Despite no significant differences among treatments for initial infiltration rates, the runoff hydrographs indicated that differences in accumulated runoff did exist among treatments (McEldowney 1999). These differences were especially evident during the early stages of runoff and contributed to the greater percentage of applied water that ran off of the grazed plots, when compared with the trampled, mowed, or control plots (Table 1). Results also indicated that equilibrium runoff was not greatly influenced by the treatments, suggesting that these early periods of runoff may provide more insight into the effects of various types of surface disturbances on overland flow.

For example, Packer (1953) determined that simulated trampling within the Boise River watershed in Idaho increased overland flow in 2 community types with initial ground cover values less than 90 to 95%. In a 10 year study conducted near Grand Junction, Colo., Lusby (1970) noted grazed watersheds had 30% more runoff than did ungrazed watersheds. He believed that increased runoff was directly related to the amount of bare soil. Heavy continuous grazing on small mixed shortgrass and midgrass prairie watersheds in South Dakota resulted in higher runoff rates than from moderately and lightly grazed watersheds (Hanson et al. 1970). Total runoff was greater from heavily grazed shortgrass prairie as compared to lightly grazed areas in eastern Colorado (Frasier et al. 1995).

The parameters that best predicted the amount of accumulated runoff after 1 hour were stem density, rainfall intensity, and a slope-gradient by area-interaction. The prediction model for accumulated runoff shown in Table 2 explained 75% of the measured variability. Inclusion of rainfall intensity and the topographic interaction between slope and area in this regression model was expected, as these variables are common parameters in many models of runoff, erosion, and water quality (Schreiber and Kincaid 1967, Dunne and Leopold 1978, Hairsine et al. 1992, Renard et al. 1997). Reduced stem density on the grazed treatments probably allowed more water to runoff of those plots and has not been included in most runoff models.

Vegetation height was not measured in this study, but was visually homogenous throughout the study area prior to treatments. In other studies, vegetation height was an important parameter for runoff prediction (Prosser et al. 1995, Clary et al. 1996). Visual similarity in vegetation height between the control and trampled treatments suggests that vegetation on these plots was overtopped by the high intensity of simulated rainfall (Abt et al. 1993, Pearce 1995, Prosser et al. 1995), and facilitated the movement of water off of these plots.

Time to Runoff Initiation

The treatments did affect the length of time required for runoff to begin, and ranged from 9 min on the grazed treatment to 22 min on the mowed treatment (Table 1). These values were similar to runoff initiation times reported by Frasier et al. (1998b) and Fernald (1997). Multiple regression analysis revealed that rainfall intensity and stem density accounted for 84% of the total measured variability in the prediction of time to runoff initiation (Table 2).

Rising Limb of the Hydrograph

The slope of the rising limb of the hydrograph was steep for the grazed treatment (Table 1). This value was not different from the mowed treatment, but was greater than the trampled and control treatments. The slopes of the rising limb for the mowed, trampled, and control treatments were not different from one another. These slopes (regression coefficients) for the rising limb trendline of the hydrograph were generally higher than those found by Frasier et al. (1998b). Simulation intensity was 40 mm hour^{-1} greater than those used by Frasier et al. (1998b) and this was probably the reason for the difference. The rate of change of the rising limb of the runoff hydrograph is an indicator of the amount of depression storage and infiltration (Mohamoud et al. 1990, Frasier et al. 1998b). During the rising limb, depression storage has often been assumed to be completely filled (Mohamoud et al. 1990). As rainfall continues, the successive overtopping of depressions makes more water available for runoff until the majority of the plot area is contributing to runoff. A smaller, or less steep, slope of the rising limb corresponds to slower runoff rates and likely indicates the degree of connectivity among surface depressions.

Antecedent soil moisture was the most important parameter for the prediction of the slope of the runoff hydrograph rising limb (Table 2). Stem density and the RUSLE surface roughness measurement improved the prediction model and together these 3 parameters explained 65% of the variability in the prediction of the slope of the rising limb of the hydrograph. Antecedent soil moisture can affect infiltration rates and, consequently, surface runoff (Branson et al. 1981). The soil moisture gradient from lower soil moisture along the upper portion of the riparian meadow to much higher soil moisture near Sheep Creek helped to explain its importance in the regression equation developed from these data (McEldowney 1999). At the Walnut Gulch Experimental Watershed in southern Arizona, Schreiber and Kincaid (1967) concluded that antecedent soil moisture was not as important as plant parameters in runoff prediction. Inclusion of random roughness in our prediction model during this early stage of runoff indicated that the volume of water applied had not yet completely overwhelmed microtopographical features, and emphasized the importance of microrelief on the early stages of overland flow initiation.

Time to Equilibrium Runoff

The time required to reach equilibrium runoff was affected by the treatments, and ranged from 16 min for the grazed treatment to 35 min for the mowed treatment. All treatments were significantly different from one another (Table 1). Rainfall intensity and stem density strongly influenced the time needed to reach equilibrium runoff. These 2 parameters accounted for 59% of the total variability for the time to runoff equilibrium (Table 2). Both rainfall intensity and stem density have already been discussed, and were applicable to the prediction model for time to equilibrium runoff for reasons stated earlier.

Slope of the Falling Limb of the Hydrograph

Significant differences were found between the 2 cattle treatments and the mowed treatment for the slope of the falling limb of the hydrograph (Table 1). However, the slope of the falling limb for the trampled treatment was not different from the control. A potential reason for this was that the tall vegetation on the control and trampled treatments was pushed over by the intense rainfall or cattle trampling, creating a surface conducive to runoff (Abt et al. 1993, Pearce 1995, Prosser et al. 1995). Both the falling limb of the trampled and control treatments were fairly steep as this water ran off rapidly once the simulator was turned off. The runoff hydrograph falling limb for the trampled and control treatments did not decline as rapidly as that from the mowed treatment, nor as slowly as that from the grazed treatment.

The runoff hydrograph falling limb represents the portion of the applied water on the plot surface that only runs off once the simulator is turned off and rainfall ends. Therefore, the falling limb can be used as an indicator of water storage on the surface (Foster 1971, Dunne and Leopold 1978, Rogers and Singh 1986) and in the soil. More water moved off the cattle-treated plots and did not infiltrate into the soil, which contributed to the flattened slopes of the falling limb of the cattle-treated plots in the runoff hydrograph (Table 1).

The prediction model for the slope of the falling limb of the hydrograph was best described by stem density and sedge ground cover ($r^2 = 0.52$) (Table 2). Sedge ground cover did not differ among treatments, but was very different among blocks. The regression equation indicated that as sedge ground cover increased, the slope of the falling limb of the hydrograph was greater.

Summary and Conclusions

This study improves our understanding of flow and runoff processes following cattle use of montane riparian ecosystems. Vegetation stem density was greatly reduced on cattle-treated plots and was a major factor that affected flow characteristics. Studies by Rogers and Schumm (1991) showed that vegetation disrupts overland flow by both concentrating and deflecting flow around individual vegetation obstructions. Specifically, forb stem density appeared to be the most influential vegetation class affecting the various flow parameters in the current study. Forbs had the greatest basal widths of stems and probably affected downslope flows by diverting water. Forbs were also possibly more susceptible to cattle trampling than graminoids.

Cattle grazing and trampling had a significant effect on flow characteristics through decreased microchannel sinuosity and drainage density, and increased flow depths. Water flowed down the plots in small channels, though sheetflow did occur between these microchannels for short distances with high water application rates. Cattle grazing and trampling straightened the microchannels, and this decreased sinuosity resulted in decreased drainage density. On cattle-treated plots, water concentrated in fewer, straighter microchannels, resulting in deeper flow depth and possibly increased flow velocities. With less ground cover, concentrated flow increases flow velocity and depth (Rogers and Schumm 1991). Velocity is a function of channel gradient and roughness, so with decreased sinuosity and greater gradient following cattle treatments as well as decreased roughness from stem density, greater flow velocities should occur. Control and mowed plots had more sinuous flow paths compared with cattle-treated plots because there was no decrease in stem density, thus more obstacles were present at the soil surface to route water around.

Changes in vegetation and flow characteristics may have consequences for erosion and effectiveness of riparian filters. Densely covered grasslands provide resistance, expressed as a threshold of shear stress, to erosion by overland flow. Most shear stress is exerted on individual plant stems and dense bunches of grasses (Prosser et al. 1995). Dillaha et al. (1989) suggested that unless concentrated flow is minimized in vegetation filter strips (VFS), it is unlikely the VFS will be very effective in controlling nonpoint source pollution.

Stem density was also one of the most important factors affecting runoff. Cattle grazing reduced total stem density, which reduced this friction component and created a surface less resistant to overland flow. These results suggest that closely monitored stem density could help to create an optimal situation for water retention and reduction of overland flow. It is important to note that the high water application rate used in this study caused the plots to be almost completely inundated with water. At lower levels of inundation, stem density might have less influence on runoff.

Abiotic factors that affected runoff prediction were rainfall intensity, slope, plot area, and soil moisture. Rainfall intensity was especially important for runoff initiation, as expected. High intensity-high frequency cattle grazing primarily impacted the initial and final stages of runoff. Runoff initiation was more rapid and leveled off quickly on grazed plots when compared with control plots. These differences resulted in greater accumulated runoff from grazed plots.

In this study, high intensity-high frequency cattle grazing created a more uniform flow regime across the trampled and grazed treatments. The microchannels became wider and tended to be less sinuous. Because the effectiveness of riparian buffers is often dependent on uniform flow, careful management of cattle along the upper edges of a riparian buffer may help to create a more uniform flow distribution entering the buffer, which could lead to improved sediment filtration.

This study was designed to better understand the effect of the cattle grazing and trampling on the factors that affect runoff in a riparian zone. The study was designed to maximize this effect, and it would be expected that with normal management practices the impact of the cattle would be less than we measured. It was a study at one place and time and results would be expected to apply to other sites with similar soils and vegetation composition.

Further research of flow processes will better allow us to quantify the effects that cattle have on riparian surface hydrology and sediment delivery to streams. Additionally, studies such as this one may be important in erosion prediction models or the development of a riparian-specific erosion model. Future studies in different riparian communities using lower simulation rates should be conducted to corroborate or refute the results presented here, and to expand the applicability of these findings. The effects of different grazing intensities and timing of grazing disturbance on stem density, microtopography, and runoff hydrographs in various riparian ecosystems also should be quantified.

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Seed recovery and germination of reseeded species fed to cattle

K. M. DOUCETTE, K. M. WITTENBERG, AND W. P. McCAUGHEY

K. M. Doucette(undergrad student) and K. M. Wittenberg (Professor), Department of Animal Science, University of Manitoba, Winnipeg Manitoba, R3T 2N2. W. P. McCaughey (Scientist), Agriculture and Agri-Food Canada, Research Centre, P. 0. Box JOOQA, Brandon, Manitoba R7A 5Y3. Corresponding author: K. M. Wittenberg

Abstract

Cattle have the potential to act as a low cost alternative for seed dissemination of valuable native species. Data collected from this trial was used to compare seed recovery, rate of passage and viability following ingestion and excretion of 7 plant species. Woods rose (*Rosa woodsii* Lindl.), snowberry (*Symphoricarpos albus* L.), purple prairie clover (*Petalostemom purpureum* Vent.), birdsfoot trefoil (*Lotus corniculatus* L.), western wheatgrass (*Pascopyrom smithii* Rydb A. Love, formerly known as *Agropyron smithii* Rydb.), green needlegrass (*Nassella viridula* Trin.), and yellow coneflower (*Ratibida columnifera* Nutt.) seed was used in the study. Two steers were fed a seed-free diet consisting of fresh cut vegetative Kentucky bluegrass (*Poa pratensis* L.)-alfalfa (*Medicago sativa* L.) forage. Following a 13 day adjustment period to the diet, steers were fed a single dose of a known number of seeds, and total feces collection was conducted for 168 hours post dosing. Fecal sub-samples were subjected to a stacked screen washing procedure for seed recovery and analysis. Seeds from both pre- and post-ingestion were tested for hard seededness, firm ungerminated seed, and germination. Seed recovery varied between seed types, ranging from 5.9% of total ingested seed for western wheatgrass, to 86.3% for Woods rose. Excretion patterns for ingested seed varied between seed types, with 50% of excreted seed being recovered between 30 to 54 hours post-dosing. Seed ingestion and passage through the digestive tract reduced viability. Cattle dissemination of viable seeds (as a % of ingested) such as Woods rose (77.4) and snowberry (69.3), would be a feasible method of delivering large numbers of viable seeds onto selected areas. Dissemination of birdsfoot trefoil (17.5), green needlegrass (11.9), and purple prairie clover (7.2), yellow coneflower (3.8), and western wheatgrass (1.3), using cattle would be less efficient, implementation should be based on seed access and cost.

Key Words: seed dispersal, cattle digestion, passage, dissemination, seed survival

Resumen

El ganado tiene el potencial de actuar como una alternativa de bajo costo para la diseminación de semilla de especies nativas valiosas. Los datos colectados de este ensayo fueron utilizados para comparar la recuperación de semilla, la tasa de paso y la viabilidad de la semilla después de ingerida y excretada y se estudiaron 7 especies de plantas. En este experimento se utilizo semilla de "Woods rose" (*Rosa woodsii* Lindl.), "Snowberry" (*Symphoricarpos albus* L.), "Purple prairie clover" (*Petalostemom purpureum* Vent.), "Birdsfoot trefoil" (*Lotus corniculatus* L.), "Western wheatgrass" (*Pascopyrom smithii* Rydb A. Love, formerly known as *Agropyron smithii* Rydb.), "Green needlegrass" (*Nassella viridula* Trin.) y "Yellow coneflower" (*Ratibida columnifera* Nutt.). Dos novillos se alimentaron con una dieta libre de semilla consistente de forraje fresco de "Kentucky bluegrass" (*Poa pratensis* L.) cortado en etapa vegetativa + "Alfalfa" (*Medicago sativa* L.). Después de un periodo de 13 días de adaptación a la dieta, los novillos se alimentaron con una sola dosis de un número conocido de semilla y se condujo una colección total de heces durante 168 horas después de administradas las semillas. Submuestras fecales se sometieron a un procedimiento de lavado a través de mallas apliadas para recuperar la semilla y su análisis. Antes y después de la ingestión se evaluaron las semillas para determinar su dureza, semillas sin germinar y germinación. La recuperación de semilla difirió entre tipos de semillas, variando en un rango de 5.9% del total de la semilla ingerida del "Western wheatgrass" al 86.3% para el "Woods rose". Los patrones de excreción de la semilla ingerida variaron entre tipos de semilla, el 50% de recuperación de la semilla excretada ocurrió entre las 34 a 54 horas de consumida la semilla. La ingestión de semilla y su paso a través del tracto digestivo reducen la viabilidad. La diseminación de semilla viable por el ganado (como % del ingerido) sería, en el caso de "Woods rose (77.4) y "Snowberry" (69.3), un método factible para depositar grandes cantidades se semilla viable en áreas seleccionadas. Para el caso de "Birdsfoot trefoil" (17.5), "Green needlegrass" (11.9), "Purple prairie clover" (7.2), "Yellow coneflower" (3.8) y "Western wheatgrass" (1.3) la diseminación de semilla utilizando ganado sería menos eficiente y la implementación debe basarse en el acceso a la semilla y su costo.

Many seed dispersal mechanisms exist for plants using wind, water, and animals as the dispersal agents. Researchers have noted that successful dissemination of seeds through cattle feces is common (Welch 1985, Pleasant and Schlather 1994). Early work by Ridley (1930) identified 124 species for which successful seed dispersal by cattle was documented.

Burton and Andrews (1948) and Lyon et al. (1992) examined the dissemination of weed seeds by cattle and observed that this method of dissemination is successful enough to be a cause for concern in monoculture farming or managed ecosystems. Many studies have examined the mechanism of weed seed dispersal via

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the animal digestive tract, but less research has examined animals as a vehicle for the dissemination of desirable species (Simao Neto et al. 1987, Barrow and Havstad 1992, Ocumpaugh et al. 1993).

Seeding desired species into select areas is highly desirable, often leading to an improvement in forage productivity, wildlife habitat, soil, and water quality. When attempting to revegetate large inaccessible areas of land, mechanical seeding methods may have limited success or may not be possible (Barrow and Havstad 1992), while manual reseeding is extremely time consuming and expensive (Ocumpaugh et al. 1996). Cattle ingestion and excretion of seed as a method of seed dispersal has potential to transport large numbers of seeds and deposit them in a germinable form into an environment suitable for establishment. Ocumpaugh et al. (1996) suggested the advantages of fecal seeding for species compatible with this method of dispersal include higher seedling emergence, establishment and growth. Reintroduction of native plant species for improvement of wildlife habitat is being considered on selected sites across the Canadian Prairie. The objective of this study was to determine whether this method is biologically feasible for revegetation programs involving Woods rose (*Rosa woodsii* Lindl.), snowberry (*Symphoricarpos albus* L.), purple prairie clover (*Petalostemom purpureum* Vent.), birdsfoot trefoil (*Lotus corniculatus* L.), western wheatgrass (*Pascopyrom smithii* Rydb. A. Love, formerly known as *Agropyron smithii* Rydb.), green needlegrass (*Nassella viridula* Trin.), and yellow coneflower seeds (*Ratibida columnifera* Nutt.). These plants, with the exception of birdsfoot trefoil, represent native forbs, grasses, shrubs and woody plants in the Northern Great Plains.

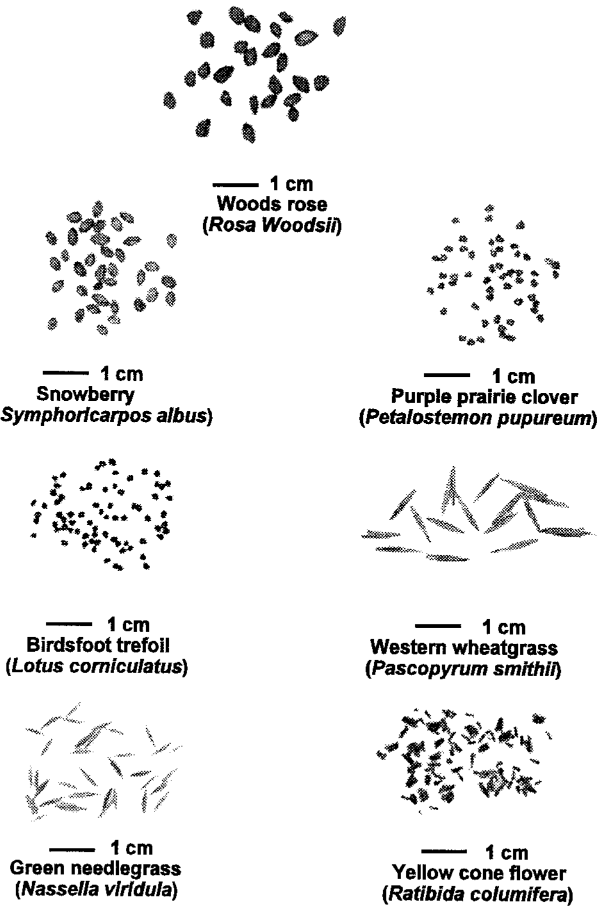

Fig. 1. Sample of seeds fed to growing steers.

Materials and Methods

Seeds from Woods rose, purple prairie clover, snowberry and green needlegrass were hand harvested and cleaned by air separation and hand sieving (Fig. 1). Seed from yellow coneflower was hand harvested and did not require further cleaning. Western wheatgrass was mechanically harvested and cleaned by sieving. Birdsfoot trefoil was purchased as cleaned seed from a commercial seed supplier. The seed was harvested from several locations in southern Saskatchewan at 50°26' N, 103° W. Seeds were hand mixed using methods described by the Association of Official Seed Analysts (1993, method 2.2). Sub-samples were obtained for seed characterization and animal dosing. Seed density and number of seeds g^{-1}, were established by counting seeds of a known weight using 5 replicates. Quantity of seeds to be fed was determined by the seed size, and ease with which it could be identified in the feces.

Three Holstein steers, weighing 580 ± 9kg, and accustomed to ground barley supplementation were housed in floor pens for 11 days while adapting to a diet of green chopped vegetative Kentucky bluegrass (*Poa pratensis* L.)-alfalfa (*Medicago sativa* L.) forage mixture (70:30, DM basis) which was fed 1.5% of body weight. Fresh water and cobalt-iodized salt licks were available ad libitum. Steers were relocated to metabolism crates on day 12 and allowed to adjust to the crates. Seed from the 7 plant species were fed to each steer on day 14 of the trial. Animals were handled in accordance with guidelines established by the Canadian Council on Animal Care (CCAC 1993).

Green chop forage was harvested every second day using a Haldrup harvester and was stored in large plastic containers in a cooler kept at 3°C. Forage was harvested at the vegetative stage to prevent mature seed ingestion by the steers. Fresh forage was used to create a rumen environment similar to that of grazing animals.

Samples of the fresh forage were obtained at each feeding and were stored (–20° C) for dry matter (DM), crude protein (CP), neutral detergent fiber (NDF), and acid detergent fiber (ADE) determination at a later date. Samples were composited, placed in a forced air oven at 60°C for 48 hours, then ground to pass a 1 mm screen prior to analysis for DM, CP (Kjeldahl method, Method No. 984.13, AOAC 1990; using a Tecator 1030 analyzer), NDF (Goering and Van Soest 1970) and ADE [Method No. 973.18, AQAC 1990; using ANKOM's Fiber Analyzer #F200 (Fairport, N.Y.)].

Animals were maintained in metabolism crates at the time of seed dosing and during the 8 day total fecal collection period. Steers were exercised twice, at 50 and at 98 hours post dosing during the fecal collection period. Feces excreted during the exercise period was collected. Steers were fed half of their daily forage allotment the evening of day 13 and on day 14 at 0920 hours the steers were offered 1,854 g of seeds mixed in 1 kg of ground barley. The seed mixture was left in the feed bunks for 6 hours. After 6 hours the remaining seed-barley mixture was collected, weighed, and analyzed for DM and seed content. Green chop forage was offered at 1.5% BW thereafter, and for the following 7 days.

Feces were collected in plastic trays. Total feces in the tray was weighed, mixed and sub- sampled at 6, 12, 24, 30, 36, 42, 48, 54, 60, 66, 72, 84, 96, 108, 120, 132, 144, 156, and 168 hours after the seed was first offered to the steers.

Feces collected from each steer within a period from the 6 hour to 72 hour collections were mixed for 10 minutes on low speed in a Hobart mixer (Model lt 600, spec 6345, Hobart Manufacturing Co. Ltd., Toronto, Canada) prior to sampling. The subsequent 12 hour collection samples from each steer were mixed individually for 15 minutes prior to sampling. Five, 200 g aliquots were sampled for each steer by collection time. One aliquot was retained for DM determination, 2 for germination assays, 1 for seed recovery estimates and another was stored at –20°C for nitrogen determination at a later date. Seed offered, seed not consumed, and feces DM determinations were conducted after 48 hours drying in a forced air oven at 60°C. Dried fecal samples were ground to pass a 1 mm screen and sent to Norwest Labs, 545 University Crescent, Winnipeg, Manitoba, for nitrate-N analysis (Greenberg et al. 1995, method 4500-N).

Seed recovery was conducted using a method similar to Jones and Bunch (1977). A 200 g fecal sample was placed in a 2 liter container. One liter of water was added to the feces and gently stirred to create a slurry. The slurry was then poured through a series of 3 stacked sieves with decreasing apertures of 2 mm, 1 mm, and 0.42 mm (Mesh #10,18 and 40, U. S. Standard Sieve Series, Endecotts (Filters) Limited, London, England). Sieves were rinsed with water until the majority of the fine particles washed away. The seeds remained in the sieves along with the larger particles of digesta. The residue from each screen was transferred separately to trays lined with paper towel, and dried for approximately 24 hours at 28° C in a forced air oven. Dried samples were sieved gently through a 2 mm sieve to break up any clumps.

A forced air aspirator (E. L. Ericson Products, Brookings, S. D. USA, Model D, Serial #175) with controllable airflow was used to separate the finer particles from the dried seeds. All fractions of the dried feces were carefully examined with the use of a magnifying lamp and stereoscope. All recognizable seeds, regardless of physical damage, were retrieved and separated according to seed type. Seed counts were conducted using the sorted material.

Based on total fecal collection and seed densities from the 200 g sub sample, seed recovery at time (t) was calculated as:

((Seeds ÷ 200 g sub-sample) x (total g fecal output (time t)) ÷ original number of seeds ingested)*l00.

Seed viability was determined to be the sum of hard seeds or firm ungerminated seeds and the normal seedlings emerged as a percent of total seed. One hundred seeds representing each species at each collection time were sent to Accutest Seed Labs (Box 579, Rivers, Manitoba, Canada, ROK lXO, Marie Greeniaus, accredited seed analyst) for germination analysis based on standard germination trials by the Association of Official Seed Analysts (1993). Seeds were tested for viability, percent hard seededness (legumes and shrubs), percent firm ungerminated seed (grasses, forbs, and woody plants), and ability to germinate. Some fecal samples did not yield 100 seeds per species, in which case all collected seeds were submitted.

The effect of seed type on seed recovered, viable seed recovered and normal seed germination was analyzed as a one-way analysis of variance using SAS Institute, Inc. (1988). Statistical differences among treatment means were tested using the Student-Newman-Keuls test when seed type differences were observed. Correlations were performed for seed viability vs retention time in the digestive tract for each seed type.

Results and Discussion

Woods rose, the heaviest of the 7 seeds, had a seed weight of 13.6 mg, and is characterized as a smooth, round unhulled shrub seed which exhibited a high degree of hard seededness (Table 1). Snowberry,

Table 1. Characteristics of seed fed to growing steers.

Scientific Name	Common Name	Plant Type	100-seed weight	Viability[1]	Hard seed[2] (H) I Firm ungerminated[3] (F)	Normal seedlings[4]
			(mg)	(%)	(%)	(%)
Rosa woodsii	Woods rose	Shrub	1360	100	100 H	0
Symphoricarpos albus	Snowberry	Woody plant	460	94	94 F	0
Petalostemon puipureum	Purple prairie clover Forb/legume	Warm season	170	91	9 H	82
Lotus corniculatus	Birdsfoot trefoil	Legume	120	89	21H	68
Pascopyrum smithii	Western wheatgrass	Cool season Grass	340	65	52 F	13
Nassella viridula	Green needlegrass	Cool season Grass	170	68	42 F	26
Ratibida columnifera	Yellow coneflower	Forb	70	44	1 F	43

[1] Viability; percent hard seed or firm ungerminated + percent normal seedlings

[2] Hard seed; seed which remains hard at the end of the prescribed test period because it has not absorbed water due to an impermeable seed coat (Association of Official Seed Analysts 1993)

[3] Firm Ungerminated Seed; seed which has failed to germinate but has imbibed moisture and appears firm, fresh, and capable of germination at the end of the prescribed test period and under prescribed test conditions. Such seeds may be viable but dormant (Association of Official Seed Analysts 1993)

[4] Normal seedlings; Seedlings possessing the essential structures that are indicative of their ability to produce useful mature plants under favorable field conditions (Association of Official Seed Analysts 1993)

had a seed weight of 4.6 mg, and is classified as a woody plant. It had a relatively smooth tear-shaped seed without a hull or awns and exhibited a high degree of firm ungerminated seeds. Purple prairie clover and birdsfoot trefoil, both legumes, had round, smooth seeds without hulls or awns. Seeds of those species weighed 1.7 mg and 1.2 mg, respectively. Both purple prairie clover and birdsfoot trefoil seeds had a low level of hard seeds. Birdsfoot trefoil seed can be as high as 90% hard seed, but scarification during seed harvest and processing will reduce the percent hard seed (Beuselinck and Grant 19957 Western wheatgrass and green needlegrass are both cool season grasses with elongated seeds. Western wheatgrass produced a bulky, hulled seed with a weight of 3.3 mg and exhibited 52% firm ungerminated seeds while green needlegrass had a smooth seed with a seed weight of 1.7 mg and exhibited 42% firm ungerminated seeds. Yellow coneflower, a forb, had hulled tear-shaped seeds with a bulky hull and a seed weight of 0.7 mg. Yellow coneflower exhibited very low levels of firm ungerminated seeds.

In general, the Woods rose, snowberry, purple prairie clover and birdsfoot trefoil seeds were rounder than the elongated western wheatgrass, and green needlegrass (Figure 1). Woods rose, snowberry, purple prairie clover, birdsfoot trefoil, and green needlegrass seeds were smoother and more dense than the western wheatgrass and yellow coneflower seeds, which exhibited a builder hull.

The green chopped vegetative Kentucky bluegrass-alfalfa forage fed to steers averaged 32% DM and contained 13.6% CP, 55.5% NDF and 36.4% ADF, DM basis. Seed consumption varied considerably among the 3 steers. One steer, #27, consumed 484 g or 17% of the 2,8S4 g seed-barley mixture offered. A second steer, #36, rapidly consumed 2,822 g or 99% of the seed barley mixture, whereas the third steer, #29, consumed 2,029 g or 71% of the seed barley mixture within 6 hours. If animal dispersal of seeds is to be used as a tool for revegetation using a dose feeding system, a high 23 degree of variation can be expected in seed intake by the animals that are to serve as "seeders", even though they had been accustomed to grain supplementation. This problem can be avoided by dosing the animals with gelatin capsules containing the desired seed, however, that option is not considered suitable when larger volumes of seed are being considered as in this study. With the limited number of animals used in our study, it is not possible to evaluate the causes of animal-to-animal variation.

Animals in the current trial were intake restricted to 50% of the regular intake of 1.5% body weight on a DM basis in the 24 hours immediately prior to feeding the seed-barley mixture. More rapid and more uniform intake may have been realized if a more severe feed restriction had been imposed. A severe feed restriction was not used in the current trial because it would have influenced the rate of passage. Due to low ingestion of seed, data were not collected for steer #27.

Woods rose (86 ± 3%) and snowberry (84 ± 3%) had the highest ($P < 0.05$) recovery, as a percentage of seed ingested (Table 2). Recovery of seed did not differ ($P > 0.05$) for western wheatgrass (6 ± 3%), yellow coneflower (18 ± 3%), purple prairie clover (26 ± 3%), green needlegrass (26 ± 3%), and birdsfoot trefoil (27 ± 3%). Woods rose and snowberry had a greater percentage of hard seed or firm ungerminated seed (Table 1), which appeared to result in a greater post ingestion recovery than purple prairie clover and birdsfoot trefoil. These findings are in accordance with Gardener et al. (1993) who observed a drop in seed recovery in feces from 80 to 6% as hard seed content declined from 95 % in *Leucaena leucocephala* (leucaena) to 6 % in *Trifolium repens* (white clover) of the ingested seed. Ocumpaugh (1994) noted that most cool season grasses tend to exhibit poor seed survival when exposed to ruminant digestion, an observation we found for western wheatgrass.

Rate of seed passage, expressed cumulatively, as time taken to recover 50% of seed excreted, 22 revealed that for all seed types 50% of the recovered seed was excreted within 30 to 54 hours afterseed was offered to steers (Fig. 2 and 3). Peak excretion rate of Woods rose, snowberry and green needlegrass seeds occurred from 30 to 36 hours post-ingestion. Peak excretion rate of purple prairie clover, and birdsfoot trefoil seeds occurred from 24 to 36 hours post-ingestion. Peak excretion rate of yellow coneflower and western wheatgrass seeds occurred from 42 to 48 hours and 48 to 54 hours post-ingestion, respectively.

Seed viability was lower after ingestion of the seeds (Table 2). Residence time in

Table 2. Total seed ingested, seed removed from feces, and germination results of recovered seeds when fed to growing steers.

Seed Type	Anaimal	Total seed	Seed recovered, ingested	Total viable[1] % of intake	Viable seed recovered recovered see	Total normal % of intake	Nomral seedlings seedlings
% of intake							
		(No.)	(%)	(No.)	(%)	(No.)	(%)
Woods rose	#29	19,147	81.5	12,829	67.0	0	0
	#36	29,705	91.0	26,083	87.8	0	0
Snowberry	#29	23,887	81.0	13,812	57.8	0	0
	#36	29,840	87.3	24,065	80.7	0	0
Purple prairie clover	#29	130,458	16.7	3,893	3.0	1176	0.9
	#36	148,918	34.5	16,996	11.4	1936	1.3
Birdsfoot trefoil	#29	128,796	16.7	11,016	8.6	645	0.5
	#36	148,937	36.3	39125	26.3	2667	1.8
Western wheatgrass	#29	117,678	7.1	1,666	1.4	205	0.2
	#36	149,522	4.6	1,732	1.2	92	0.1
Green needlegrass	#29	125,633	29.6	15,105	12.0	2063	1.6
	#36	149,396	22.1	17,606	11.8	1435	1.0
Yellow coneflower	#29	129,445	19.6	5076	3.9	4479	3.5
	#36	149,378	16.3	5552	3.7	3495	2.3

[1] Viability; percent hard seed or firm ungerminated + percent normal seedlings.

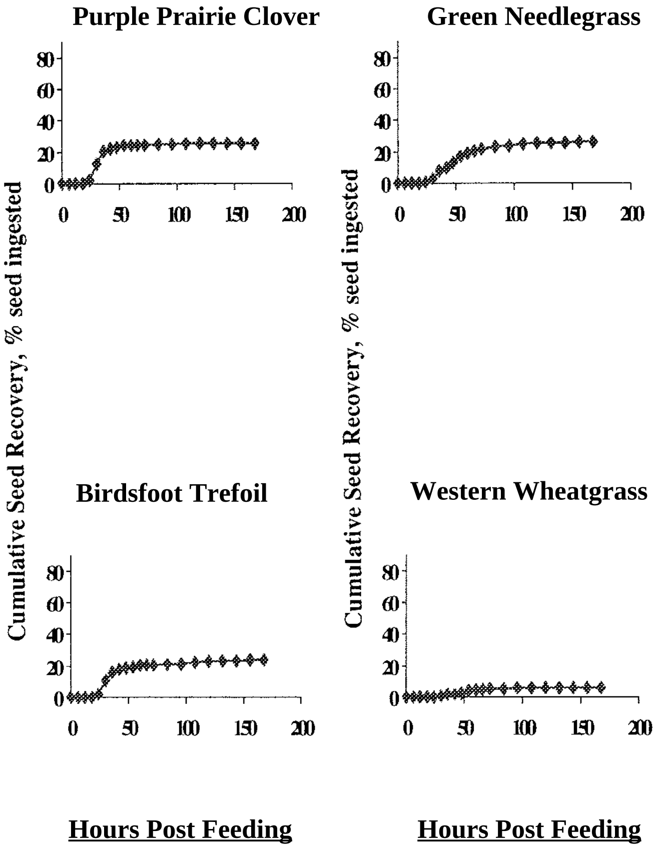

Fig. 2. Fecal recovery over a 7-day period for legume and grass seeds ingested as a single dose by steers. n = 2

the digestive tract did decrease (P < 0.05) seed viability for western wheatgrass, green needlegrass and yellow coneflower; however, this trend was not apparent for the other seed types (Table 3). Some of the recovered Woods rose seed showed signs of physical damage, probably due to mastication. Recovered snowberry seed showed minimal signs of physical damage, however, some seed coats were removed and the seeds appeared lighter in color. When recovered purple prairie clover seed was examined it was observed that there was extensive physical damage to the seed. Many seed coats were removed and some of the seeds began germination in vivo. When the recovered birdsfoot trefoil seed was examined physical damage, such as seed coat loss, was observed. Recovered seed from western wheatgrass and green needlegrass did not have visible physical damage. Examination of the recovered yellow coneflower seed revealed that the majority of the seeds appeared to have had the hulls removed but no other physical damage was visible.

Although total seed recovered declined dramatically by 120 hours post ingestion, viability of seed recovered thereafter was high for some seed types. For example, 6 snowberry seeds recovered from the 144 hour fecal sample had 100% viable firm ungerminated seed. From the same fecal collection time, birdsfoot trefoil had 11 seeds recovered with 89% viable hard seed, and purple prairieclover had nine seeds with 88% viable hard seed. Simao Neto et al. (1987) have also reported thatthe percentage of viable hard seed recovered increased with time. This may be because non-viable seed with a long residence time in the digestive tract was digested. Gardener et al. (1993) also reported that for some intact seed, percent viability and hard seededness increased with time spent in the digestive tract.

The residence time of seed in the ruminant digestive tract has been negatively correlated with seed germinability (Simao Neto et al. 1987, Ocumpaugh and Swakon 1993). Woods rose, snowberry, purple prairie clover, birdsfoot trefoil, and green needlegrass seeds had smoother, denser seeds and also exhibited faster rates of passage than the less dense western wheatgrass and yellow coneflower seeds. This is in accordance with Gardener et al. (1993) who speculated that smooth seeds have a faster rate of passage because they more readily separate from the fibrous digesta in the rumen than do rough surfaced seeds. Gardener et al. (1993) also indicated that density and seed size are positively correlated to rate of passage, and Ocumpaugh et al. (1991) indicated that for grasses, seed density was positively related to seed survival. Simao Neto et al. (1987) indicated that rate of passage for longer grass seeds was slower than for more compact seeds. Both green needlegrass and western wheatgrass seeds have elongated shapes, with western wheatgrass being longer. These differences in smoothness, density, and seed shape may have resulted in the slower rate of passage for both western wheatgrass, and yellow coneflower seeds. Overall, seed size and density were not positively correlated (P > 0.05) to passage rate, as heavy large seeds such as Woods rose had similar passage rates to the smaller lighter seeds of purple prairie clover and birdsfoot trefoil (Table 1). This corre-

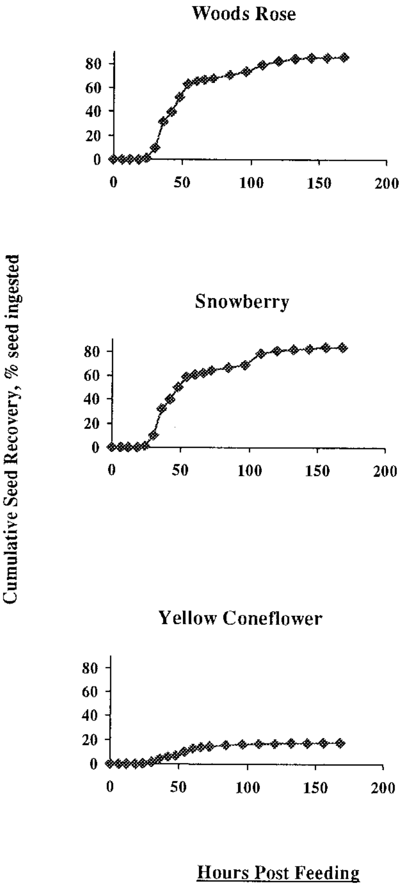

Fig. 3. Fecal recovery over a 7-day period of forb and shrub seeds ingested as a single dose by steers. n = 2

Table 3. **Effect of retention time in the digestive tract on viability (%) of seed recovered from feces. n = 2**

SeedType	1	2	3	4	5	6	7
				Retention time, days			
				(%)			
Woods Rose	100.0	96.0	92.0	95.0	98.5	91.5	81.5
Snowberry	100.0	93.5	83.0	86.5	74.0	100.0	64.0
Purple prairie clover	9.0	2.0	73.0	63.0	78.0	89.0	NA
Birdsfoot trefoil	6.5	52.5	70.0	71.5	91.5	82.0	100.0
Western wheatgrass	60.0	35.0	30.0	39.0	NA	NA	NA
Green needlegrass	68.0	63.0	60.0	42.5	51.0	42.0	11.0
Yellow coneflower	58.0	46.5	9.5	6.0	0.0	0.0	NA

NA No seeds were recovered from fecal subsamples taken in that 24 hour collection period.

sponds to work by Ocumpaugh et al. (1991) who found all seeds had similar passage rates, but contradicts work by Gardener et al. (1993) who found that large, dense seeds with low levels of hard seededness had the fastest passage rate, and high levels of hard seededness resulted in a longer mean retention time in vivo.

Excretion of viable seeds, as a percent of intake, was greatest ($P < 0.05$) for Woods rose (77 ± 3%) which had an initial viability of 100% (Table 1) and also had a high proportion of hard seed, and for snowberry (69 ± 3%) which had a high percent firm ungerminated seed pre-ingestion (Table 2). Viable seeds excreted, % of total ingested seed, did not differ ($P > 0.05$) among the other seed types. Excretion of viable seeds was least for western wheatgrass, which had an initial viability of 65%. Western wheatgrass had 52% firm ungerminated seed pre-ingestion (Table 1) and excreted seed exhibited 1.3 ± 3% viability (Table 2). Loss of seed viability was greatest for purple prairie clover which had apre-ingestion viability of9l% (Table 1) and a post digestion viability of 7.2 ± 3% (Table 2). Purple prairie clover had 9% hard seed pre-ingestion (Table 1). Birdsfoot trefoil had 21% hard seed pre-ingestion (Table 1) and excreted seed exhibited 17 ± 3% viability (Table 2). Green needlegrass had 42% firm ungerminated seed pre-ingestion (Table 1) and excreted seed exhibited 12 ± 3% viability (Table 2). Yellow coneflower had 1% firm ungerminated seed pre-ingestion (Table 1) and excreted seed exhibited 3.8 ± 3% viability (Table 2). The percentage of firm ungerminated or hard seededness was positively correlated ($P <0.05$) with seed viability post-ingestion, however, only 70% of the variation can be accounted for by measuring these seed characteristics. Low levels of seed viability for yellow coneflower and western wheatgrass could be related to increased residence time in the digestive tract and subsequent exposure to digestive processes.

It is difficult to speculate as to the cause of changes in seed viability. Jansen (1984) argues that not all plants have seeds that are adapted for seed dispersal by ungulates and would, therefore, not have the physical adaptations to survive mastication, and exposure to microbial, acid and enzyme digestion. For example, during feces collection, purple prairie clover seeds were observed to have germinated in the fresh dung. It is possible that these seeds may have begun to germinate in vivo and had these seeds been allowed to remain in the manure they would most probably have desiccated as the manure dried. This observation coupled with the low viability of recovered seed suggests that purple prairie clover would not be a species that would be suited to dispersal using grazing cattle.

Normal seedlings are defined as seedlings possessing the essential structures that are indicative of their ability to produce useful mature plants under favorable field conditions (Association of Official Seed Analysts 1993). Normal seedlings, as a percent of recovered seed, decreased due to ingestion for all seed types ($P < 0.05$, Table 2) except for Woods rose and snowberry where germination remained zero for both pre- and post-ingestion germination trials. Lengthy dormancy periods are required for Woods rose and snowberry (Gerling et al. 1996).' Results from this trial suggest that digestion does not scarify the seed or hasten germination. Yellow coneflower had low percent seed recovery and viability but had the highest ($P < 0.05$) percent of normal seedlings, expressed as a percentage of intake (2.9 ± 0.2%, Table 2).

These results coincide with studies by Yamada and Kawaguchi (1972) who reported a remarkable decrease in viability after passage through the digestive tract of cattle for ladino clover (*Trifolium repens* L., 72%), sub clover (*Trifolium subterraneum*, 51%), orchardgrass (*Dactylis glomerata* L., 74%), and Italian ryegrass (*Lolium multiflorum* Lam., 73%). Simao Netoetal. (1987) and Gardener et al. (1993) reported variable results for a range of grass and legume seeds tested. Quinn et al. (1994) found that the passage of buffalograss (*Buchloe dactyloides* Nutt.) diaspores through cattle had a positive effect on germination. Therefore, it can be concluded that the effects of seed ingestion on germination vary greatly between plant species.

It is apparent that dissemination by cattle of hard seeded, or firm ungerminated species, such as Woods rose and snowberry, is a feasible method of delivering large numbers of viable seeds onto selected areas. If cattle were used to disseminate purple prairie clover, birdsfoot trefoil, western wheatgrass, green needlegrass, and yellow coneflower seeds, much smaller numbers of viable seeds would be disseminated. Results for the mechanically harvested and cleaned birdsfoot trefoil may be improved when animals graze seed heads as hard seed content will increase. It would be necessary to evaluate the benefits of this low cost seeding alternative in light of the expense of the seed lost to digestion. Consumption of seeds by cattle is not an effective method of increasing the viability of the Great Northern Plains native species that were tested in this study or birdsfoot trefoil.

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Evaluation of 3 techniques for determining diet composition

S. R. HENLEY, D. G. SMITH, AND J. G. RAATS

Authors are research assistant, Department of Zoology, Terrestrial Ecology Research Unit, University of Port Elizabeth, P.O. Box 1600, South Africa, 6000; research associate, Institute of Cell, Animal and Population Biology, University of Edinburgh, Ashworth Laboratories, The King's Buildings, Edinburgh, EH9 3JT, Scotland; professor, University of Fort Hare, Private Bag X1314, Alice, South Africa, 5700.

Abstract

A comparative study was made of 3 techniques applied to the study of herbivore diet selection, namely direct observation, faecal analysis and the recently developed remote control oesophageal fistula valve, using 3 animals over 4 study days. Direct observation showed a relatively high level of precision with respect to the woody forage class but a poor measurement of the grass class. The ratios of grass to dicot were similar in the diets determined by direct observation and valve fistulation, but faecal analysis over-emphasised dicots relative to the other techniques. The greatest overlap in estimated diet was between faecal analysis and valve fistulation. Overall the valve fistulation technique was considered superior to the other 2 techniques because it provided reliable estimates of diet composition that could be readily equated to range conditions at the time of ingestion.

Resumen

Se realizo un ensayo comparativo de 3 técnicas aplicadas para estudiar la selección de la dieta de los hervíboros, las técnicas evaluadas fueron: observación directa, análisis fecal y la recién desarrollada válvula de la fistula esofágica de control remoto; se utilizaron 3 animales en 4 días de estudio. La observación directa mostró un nivel relativamente alto de precisión con respecto a los forrajes leñosos, pero una pobre medida de clase de zacates. Las proporciones de zacates a dicotiledóneas fueron similares en las dietas determinadas por observación directa y la fistulación de válvula, pero el análisis fecal sobrestimo las dicotiledóneas en relación a las otras técnica. El mayor traslape en la dieta estimada se dio entre el análisis fecal y la fistulación de válvula. En general, la técnica de fistulación de válvula se consideró superior a las otras dos técnicas porque provee estimaciones confiables de la composición de la dieta que pudieran ser fácilmente comparadas a las condiciones del pastizal al momento de la ingestión.

Key Words: Microhistological analysis, goats, South Africa, *Oesophageal fistula*

Quantitative analysis of the botanical composition of herbivore diets is generally determined using either direct observation of the foraging animal; examination of epidermal fragments by faecal analysis; or examination of epidermal fragments in oesophageal extrusa (Gordon 1995). Comparisons of these 3 techniques have, in the past, shown poor correlation (Vavra et al. 1978, Sanders et al. 1980, McInnis et al. 1983).

Although both faecal analysis and direct observation can provide reliable estimates of diet composition (Holechek et al. 1982a) oesophageal extrusa is considered to provide a more representative analysis of the actual composition (Forwood et al. 1987) because:

1. Oesophageal extrusa is more truly representative of the diet than direct observation because an animal has actually ingested the sampled forage (Le Du and Penning 1982) thus observer errors are eliminated and bite size need not be estimated.
2. Digestive processes that bias faecal analysis toward indigestible diet constituents are avoided (Vavra and Holechek 1980).
3. Oesophageal extrusa is less likely to be influenced by observer training and capability than faecal analysis (Holechek et al. 1982b).

Recently however, the reliability of the oesophageal extrusa samples for animals foraging within diverse plant communities has been questioned (Jones and Lascano 1992). The principal source of error is that oesophageal extrusa samples are collected only once per day, generally in the morning, after a period of fast (Coates et al. 1987). The collection of a single sample assumes that diet selection and plant species preferences remain constant throughout the day. As herbivores are likely to pass through several micro-communities of plants throughout the day, this assumption is likely to be ill-founded. Furthermore, animals that have been fasted are unlikely to select the same plants or plant parts as animals that are close to satiety (Jones and Lascano 1992). The poor reliability of oesophageal extrusa from fistulated animals has been demonstrated by Coates et al. (1987) and Jones and Lascano (1992) using a technique that discriminates between tropical legumes and tropical grasses (Ludlow et al. 1976).

The development of a remote controlled oesophageal fistula valve by Raats and Clarke (1992, 1996) has allowed oesophageal extrusa samples to be collected throughout the day without having to restrain the fistulated animal. Increasing extrusa sampling frequency with the aid of an oesophageal fistula valve improves the agreement between the grass content of diets measured by the oesophageal extrusa and direct observation techniques (Raats et al. 1996).

The development of the remote controlled oesophageal fistula valve provides an opportunity to re-evaluate the 3 techniques for estimating botanical composition. This paper presents the results of an evaluation study carried out at the University of Fort Hare, South Africa in which the direct observation, faecal analysis and

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oesophageal extrusa (obtained from goats fitted with remote controlled oesophageal fistula valves) techniques were compared.

Materials and Methods

Each technique was applied concurrently to the same 3-individual Boer goats (*Capra hircus*). The 3 goats were surgically prepared with oesophageal fistulae according to the technique described by Raats et al. (1996). The large fistula required (1,050 mm^2 aperture size) to fit the oesophageal fistula valve was achieved by stretching a standard, surgically established fistula (500 mm^2) with progressively larger plastic inserts. Following a 10 week recovery period, which included a 4 week training period to accustom the animals to the equipment and handling procedures, the goats were penned over-night in a holding pen close to the study site and were allowed to forage on a paddock that was similar and adjacent to the study site.

The study site consisted of a single paddock enclosing 1 ha of False Thornveld (Acocks 1975), rested for 1 growing season and situated on the research farm of the University of Fort Hare, South Africa (32°49'S, 26°51'E) at an altitude of 600 m. Annual rainfall was between 227 mm and 967 mm, with distinct bimodal peaks in March and October. The vegetation of the area was dominated by thorny shrubs such as *Scutia myrtina* (Burm. f.) Kurz, *Grewia occidentalis* L., *Acacia karroo* Hayne with open areas between bush clumps dominated by grasses species such as *Digitaria spp. Sporobolus spp, Themeda triandra* Forssk., *and Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy*;* few forbs were recorded. The study was carried out during winter (August) 1993, when climatic conditions were dry and cold and most plant growth had ceased.

Animals were released into the paddock between 0700 and 0800 hours and then herded back to the holding pens at 1500 hours. All forage eaten during the 15 day study period was consumed during the 8 hour daily grazing period.

Direct Observation

Direct observation of the goats was carried out using the bite count method described by Risenhoover (1989). A total of 5 days of direct observation were carried out on day 1, 4, 9, 11, and 15 of the study period. The first day was used to train observers and to identify practical problems with the methodology while the remaining 4 days were used to collect data.

To cover the whole of the 8-hour daily grazing period, direct observation sessions began at 0900 hours and finished at 1500 hours. Starting on the hour, each fistulated goat was observed (for 10 minutes per hour) in a randomly determined sequence. A 5-minute transition period between observations allowed time for the next focal animal to be located, and a 15-minute rest period was provided once all 3 animals had been observed to reduce observer fatigue. The distance between animal and observer during direct observation studies was usually within 10 m, but never more than 20 m. Observers recorded animal identity, time of observation, plant species and number of bites. Where the species selected by a goat could not be identified, the bite was recorded as an unidentified grass, forb or woody plant. Observers distinguished bites from exploratory mouthing by the occurrence of both distinct head movement and the sound of the bite, as the use of auditory cues to identify prehension has been shown to give better estimates of bite count (Ungar 1996). If a single bite included more than 1 plant species, a bite was recorded for each species.

To allow comparison with the oesophageal extrusa samples, results obtained by direct observation were grouped into 3, two-hour intervals. These 3 intervals were referred to as the morning (0900–1000 hours), midday (1100–1300 hours) and afternoon (1300–1500 hours) observation sessions.

Faecal collection

In an attempt to identify faecal pellets that were derived from material ingested during the direct observation and oesophageal extrusa study days, 7–10 g of stained-chopped hay was administered to the goats via the oesophageal fistula, on the morning of each study day immediately prior to their release into the paddock. Two colours of stained hay were used, Basic Fuchsin and Methylene Blue. The colour of hay given to the goats alternated between study days.

Faecal pellets were collected rectally from each goat on the 2 mornings (24 and 48 hours after dosing) following each of the 4 study days. This was assumed to be the period of peak output of material derived from forage eaten during the study day (Castle 1956). Faecal pellets from the 2 collections were pooled to provide 1 faecal sample from each animal per study day; a total of 12 samples. The faecal samples were dried at 65°C, then 5 pellets from each sample were milled through a 1 mm screen. Ground faecal pellets were examined for the presence of stained hay to confirm that the material originated from the appropriate sampling day, then stored ready for microhistological analysis.

Oesophageal extrusa collection

On each of the 4 study days oesophageal extrusa samples were also collected. After the goats had been brought to the study site, the fistula plugs were removed and the remote control receiver harness and battery packs were fitted. Oesophageal extrusa samples were collected hourly (a total of 8 samples daily) by remotely opening the oesophageal fistula valve and allowing the extrusa to fall to the ground. The valve remained open until sufficient extrusa had been collected (1–15 minutes). Once the animal had moved away from the feeding station extrusa samples were collected from the ground (thus reducing grazing disruption to a minimum) and placed in plastic bags and stored on ice. On return to the laboratory, samples were freeze-dried and subsequently milled through a 1 mm screen. A 2 g sub-sample was retained for microhistological analysis. Samples were pooled according to sampling times equivalent to the morning, midday and afternoon direct observation sessions (see above) to give 3 oesophageal extrusa samples per animal per study day (36 samples in total).

The morning session of direct observation was compared to oesophageal extrusa collected at 0900 hours and 1000 hours, the midday direct observation session with oesophageal extrusa collected at 1100 hours and 1200 hours and the afternoon direct observation session compared with oesophageal extrusa collected at 1300 hours and 1400 hours.

Microhistological analysis

A collection of reference slides based on positively identified specimens of all the grass, forb and browse species occurring in the study area was prepared according to the method of Storr (1961), using concentrated nitric acid to remove the mesophyll tissue from the epidermis. A dichotomous key, species descriptions and photomicrograph collection was made from the reference slide library.

Faecal and oesophageal extrusa sample material were prepared, according to the method of Scotcher (1979), again using nitric acid to remove mesophyll tissue. Five slides were made up from each of the nitric acid digested faecal samples and 2 for each of the nitric acid digested fistula samples. Each of the slides was then examined by following systematic transects and counting the fragments which fell partly or entirely between parallel lines marked on the slide (the distance between lines was slightly less than 1 field of view), using a binocular compound microscope at between 40x and 200x magnification (Stewart 1967). Transects were at least 1 field of view apart to avoid counting the same plant fragment twice. The first 20 fragments of sufficient size that were encountered on each slide were identified using the key, reference slides and species description (Green 1987), if fragments could not be identified they were recorded as either unidentified grass or dicot species. From each study day, 100 (1 sample per day with 20 fragments from 5 slides) faecal epidermal fragments and 120 (3 samples per day with 20 fragments from 2 slides) oesophageal extrusa epidermal fragments per animal were identified, allowing species comprising more than 5% of the diet to be identified (Stewart 1967).

Fragments that could not be positively identified were recorded as unidentified grasses or dicots. *Eragrostis* species could not be identified at species level with confidence so they were grouped together as a genus. To reduce bias toward small readily identifiable fragments, only particles that had an area at least as large as half the field of view at 200x magnification were identified.

Data analysis

All data collected were expressed as the frequency of which a species was encountered, this allowed direct comparisons of all 3 techniques. In the case of the faecal and oesophageal extrusa samples frequency was calculated by dividing the number of times a species was positively identified in an animal's samples by the total number of microscopic observations made for that animal (expressed as percent). For the direct observation technique frequency was calculated from the number of times a species was included in a bite taken by an animal divided by the total number of bites recorded (expressed as percent). No attempt was made to correct raw data by applying weighted bite counts (Collins and Urness 1983) or differential epidermal digestibilities (Dearden et al. 1975).

The 3 techniques were compared using Kulczynski's similarity coefficient (Smith and Shandruk 1979). Analysis of variance was carried out on arc-sine transformed percentage data for 5 of the most abundant species, using a one-way model with measurement technique as the treatment factor and individual animals as the replicated experimental units. Analysis was carried out using Minitab for windows (Release 12.1)

Results

The frequency of stained hay fragments in the faecal material during the sampling period (24–48 hours after dosing) was low (median = 16.5 particles per gram of faeces DM), indicating a lack of synchronicity between samples collected for the faecal analysis and those gathered for the other 2 techniques; peak output of stained particles was between 48 and 72 hours after dosing. However, as similarity coefficients between these techniques changed little during the course of the study, there was probably little variation in the diet composition between days and therefore comparison of faecal samples, oesophageal extrusa and direct observation remains valid. In retrospect synchronicity would have been improved if faecal samples had been collected 48 and 72 hours after dosing.

The occurrence of each species and their rank determined by the oesophageal extrusa, direct observation and faecal analysis techniques is shown in Table 1. The 10 most abundant species made up 87, 89 and 93 % of the diet measured respectively by the oesophageal extrusa, direct observation and faecal analysis techniques. When the 10 most abundant, positively identified species were ranked (Table 1) distinct differences, both in species occurrence and rank were evident between techniques. Species composition determined by the faecal analysis and oesophageal extrusa techniques showed the closest similarity with 8 of the 10 most abundant species being common and a Kulczynski's similarity coefficient of 69.3. Species composition determined with faecal analysis and direct observation showed the least similarity with only 5 of the 10 most abundant species being common and a Kulczynski's similarity coefficient of 35.0. The similarity of species composition determined by the oesophageal extrusa and direct observation techniques was 6 of the 10 most abundant species being common and a Kulczynski's similarity coefficient of 46.8.

Similarity coefficients between direct observation and the other 2 techniques diminished progressively (Table 2) with study day, whereas the similarity coefficients between faecal analysis and oesophageal extrusa showed little day-to-day variation, apart from on day 11. The variation in the relative abundance of the 5 positively identified species common to all 3 techniques is shown in Figure 1. Faecal analysis showed the least amount of daily variation in diet composition particularly in the grass component of the diet.

Statistical analysis of the relative abundance of each of the 5 forage species common to all 3 methods (*Scutia myrtina, Grewia occidentalis, Rhus longispina* Eckl. & Zeyh., *Themeda triandra* and *Sporobolus fimbriatus*(Trin.) Nees) using study days as replicates are shown in

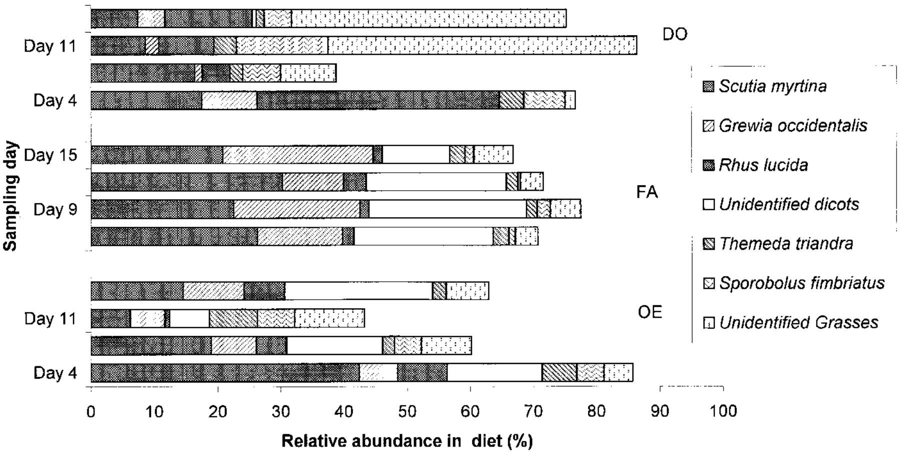

Fig. 1. Variation in the relative abundance (%) of *Scutia myrtina, Grewia occidentalis, Rhus longispina, Themeda triandra, Sporobolus fimbriatus,* unidentified grasses and unidentified dicots recorded by direct observation (DO) faecal analysis (FA) and oesophageal extrusa (OE) techniques between four sampling days.

Table 1. The relative frequency (%) and rank of species recorded by oesophageal extrusa, direct observation and faecal analysis techniques

	Oesophageal Relative frequency	Extrusa Rank	Direct Relative frequency	Observation Rank	Faecal Relative frequency	Analysis Rank
Grasses						
Eragrostis spp.	16.1	2	0.3	20	7.4	4
Unidentified grasses	7.5	4	23.3	1	5.0	5
Digitaria eriantha Steud.	4.6	7	0.6	18	1.1	11
Themeda triandra Forssk.	4.3	8	2.8	8	2.2	8
Sporobolus fimbriatus(Trin.) Nees	3.6	9	8.8	5	1.1	10
Cymbopogon plurinodis (Stapf)	2.9	10	7.1	6	0.0	—
Sporobolus africanus (Poir.)	1.7	12	0.0	—	0.9	13
Heteropogon contortus (L.) P. Beauv.	0.9	16	0.0	—	0.4	18
Panicum maximum Jacq.	0.6	18	0.1	22	0.0	—
Unnamed grass	0.6	19	0.0	—	0.0	—
Cynodon dactylon (L.) Pers.	0.3	24	0.9	14	0.4	17
Aristida congesta Roem. & Schult.	0.3	25	0.0	—	0.0	—
Total grass	43.3		43.8		18.6	
Dicots						
Scutia myrtina (Burm. f.) Kurz	20.7	1	13.3	3	26.2	1
Unidentified dicots	15.0	3	0.0	—	21.4	2
Grewia occidentalis L.	7.2	5	4.0	7 1	7.7	3
Rhus longispina Eckl. & Zeyh.	5.2	6	15.	6 2	2.	2 7
Viscum spp.	1.7	11	0.9	16	1.7	9
Rhus refracta Eckl. & Zeyh.	1.4	13	0.0	—	1.1	12
Jasminium spp.	1.4	14	0.9	15	0.0	—
Unnamed dicot 1	0.7	17	0.0	—	0.9	14
Unnamed dicot 4	0.4	20	0.0	—	4.1	6
Lippia javanica (Burm f.) Spreng.	0.4	21	0.6	17	0.6	15
Ehretia rigida (Thunb.) Druce	0.4	22	0.0	—	0.4	19
Olea europaea L.	0.3	23	9.9	4	0.4	16
Rhus undulata var. burchellii (Sond.) Schonl.	0.3	26	0.0	—	0.0	—
Lycium spp.	0.1	27	0.0	—	0.0	—
Unnamed dicot 2	0.1	28	0.0	—	0.0	—
Unnamed dicot 3	0.0	—	0.0	—	0.0	—
Maytenus heterophylla (Eckl. & Zeyh.)	0.0	—	0.0	—	0.0	—
Unnamed dicot 5	0.0	—	0.0	—	0.2	20
Unnamed dicot 6	0.0	—	0.0	—	0.1	21
Azima tetracantha Lam.	0.0	—	0.0	—	0.0	—
Acacia karroo Hayne	0.0	—	2.3	9	0.0	—
Diospyros lycioides Desf.	0.0	—	2.3	10	0.0	—
Protoasparagus spp.	0.0	—	2.3	11	0.0	—
Coddia rudis (E. Mey. ex Harv.) Verdc.	0.0	—	1.7	13	0.0	—
Unnamed forb	0.0	—	0.6	19	0.0	—
Unidentified forbs	0.0	—	0.3	21	0.0	—
Total dicots	55.5		54.5		77.1	
Aloes						
Aloe ferox Mill	1.2	15	1.7	12	8.9	4
Total number of species observed	28		22		21	

Figure 2. Differences in relative abundance measured by the oesophageal extrusa and faecal analysis techniques were only significant ($P > 0.05$) in the case of *G. occidentalis*, whilst there were no statistically significant differences between relative abundance measured with direct observation and oesophageal extrusa techniques. Differences in relative abundance as measured with direct observation and faecal analysis were significant in all cases apart from the 2 grass species *T. triandra* and *S. fimbriatus*.

Analysis of diet composition data in terms of forage type (grass, dicot, or aloe) showed that the direct observation and oesophageal extrusa techniques gave the most similar results (Table 1) with identical proportions of grass, dicot and aloe. The proportion of forage types in the diet determined by faecal analysis showed a greater proportion of dicot and aloe in the diet than the 2 other techniques, perhaps reflecting differences in epidermal digestibility between species.

The relationship between the 3 techniques is shown in Figure 2. Faecal analysis and oesophageal extrusa techniques show closest relationship with one another. Direct observation showed little relationship with the other techniques. However, in all cases there was a closer relationship of data points within than between techniques. Similarity between techniques was consistently lowest between direct observation and faecal analysis and greatest between faecal analysis and oesophageal extrusa (Fig. 2).

Discussion

Overall the faecal analysis and oesophageal extrusa techniques gave very similar results, showing close similarity in species ranking and in relative frequency. The oesophageal extrusa technique showed greater daily variation in species

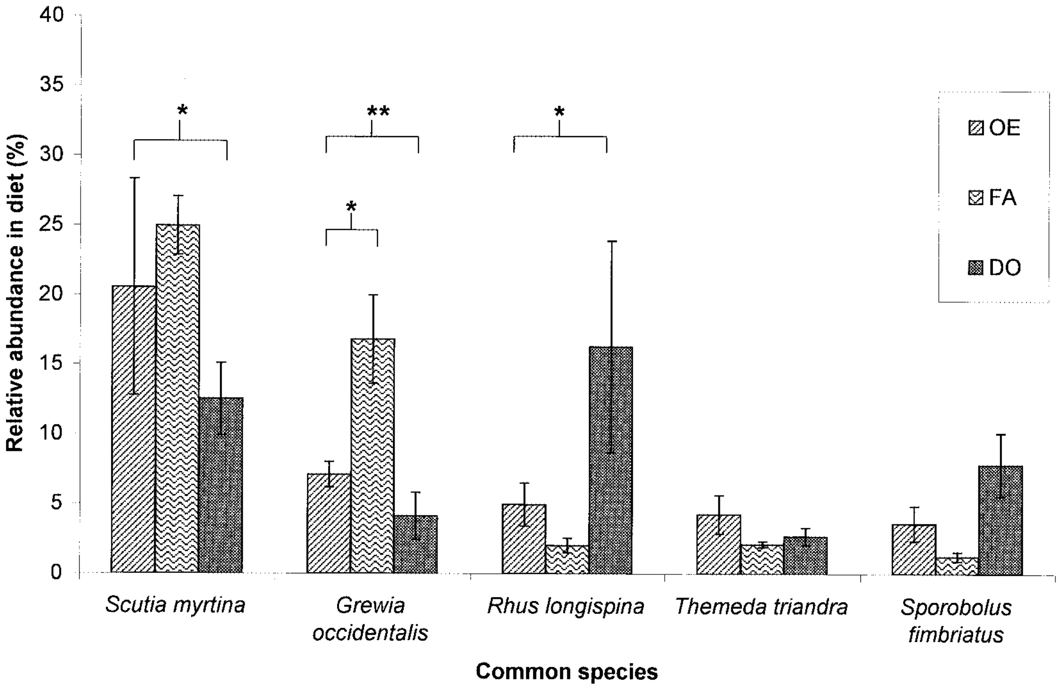

Fig. 2. Comparison of the mean relative abundance (%), with s.e., of *Scutia myrtina, Grewia occidentalis, Rhus longispina, Themeda triandra* and *Sporobolus fimbriatus* recorded by direct observation (DO) faecal analysis (FA) and oesophageal extrusa (OE), indicating significant differences between techniques. (* $P < 0.005$, $P < 0.01$)

composition of the diet than the faecal analysis technique. However, the difference between faecal analysis and oesophageal extrusa techniques could possibly be due to a different rate of passage of individual species or have been due to the lack of synchronicity between oesophageal extrusa and faecal analysis samples. This also suggests that similarities between techniques in the species ranking and relative frequency were not a consequence of them both being based on microhistological analysis.

Results obtained using the direct observation technique showed poor similarity to both the faecal analysis and oesophageal extrusa techniques. There was good agreement in forage class measurement made by the oesophageal extrusa and direct observation techniques indicating that the high occurrence of unidentifiable grasses recorded by the direct observation technique accounted for much of the lack of similarity between species composition measured by the direct observation and oesophageal extrusa techniques.

The only major difference in similarity coefficients between the faecal analysis and oesophageal extrusa occurred on day 11 of the study (Table 2). This may not necessarily reflect the greater sensitivity of the oesophageal extrusa technique to day-to day changes in diet composition, but may be a result of the small number of oesophageal extrusa samples taken per day. Oesophageal extrusa was sampled on 6 occasions per day, for periods of between 1–15 minutes. The daily oesophageal extrusa samples, therefore, represent forage that was consumed during a 6–90 minute period per day. As the number of unidentified fragments were similar for both faecal analysis and oesophageal extrusa (Table 1), faecal samples are likely to be more representative of the whole period when feed was available, because forages were comminuted and mixed during digestion before being sampled in the faeces. Comparison of the oesophageal extrusa and faecal analysis techniques based on mean relative abundance values from all 4 sampling days were only significantly different in the case of 1 species, *G. occidentalis* (Fig. 2).

Sampling frequency of oesophageal extrusa is limited because animals need to be provided with the opportunity to feed and the assumption that short-term sampling regimes are representative of the total daily intake may not necessarily be valid, especially in species-rich and patchy plant communities. Whilst the oesophageal extrusa technique has an advantage over the faecal analysis technique that correction factors for epidermal digestibility

Table 2. Comparison of the similarity in species composition (Kulczynski's coefficient) between the direct observations, oesophageal extrusa and faecal analysis techniques on study days 4, 9, 11 and 15.

Study day	Comparison	Coefficient
Day 4	Direct observation : Faecal analysis	38.3
	Direct observation : Oesophageal extrusa	43.6
	Faecal analysis : Oesophageal extrusa	64.4
Day 9	Direct observation : Faecal analysis	33.5
	Direct observation : Oesophageal extrusa	43.9
	Faecal analysis : Oesophageal extrusa	65.5
Day 11	Direct observation : Faecal analysis	22.4
	Direct observation : Oesophageal extrusa	33.5
	Faecal analysis : Oesophageal extrusa	38.2
Day 15	Direct observation : Faecal analysis	25.0
	Direct observation : Oesophageal extrusa	27.6
	Faecal analysis : Oesophageal extrusa	59.9

direct observation do not have to be applied, results obtained from a single animal on a single day do not necessarily reflect short-term changes in species utilisation.

A major distinction between the direct observation technique and the other 2 techniques was the means used to identify the species. Both the faecal analysis and oesophageal extrusa techniques relied on microhistological analysis of the samples whilst the direct observation technique relied on observers identifying the species in the field. These 2 identification techniques are likely to have distinct sources of error and different levels of both accuracy and precision.

Sensitivity of the direct observation identification method decreased as the study progressed because many of the diagnostic features of grass species, such as flower or seed-heads, diminished as a result of grazing; a similar effect was not evident with the microhistological analysis identification technique. Furthermore, browse and forb species are more readily identified than grasses by the direct observation technique; this results from the great species mix of grasses growing together and the difficulty in recognising individual species from a distance. Moreover, animals tend to spend less time per feeding station when grazing than when browsing, reducing the amount of time available to identify the plants. In the case of the microhistological technique browse and forb species are less readily identified than grasses, because of fewer diagnostic epidermal features.

The direct observation technique is also affected by differences in bite size between species unlike with the other 2 techniques. As bite size is largely determined by structural characteristics of the plant (Hodgson 1982), the use of bite count to estimate intake will overestimate the contribution of smaller leafed plants to the diets. Hence *R. longispina*, with leaf dimensions of 10–50 mm x 5–22 mm (Palgrave 1983), would be expected to have a greater relative frequency in the direct observation determined diet than in the diet determined by the faecal analysis or oesophageal extrusa techniques. Whilst *S. myrtina*, with leaf dimensions of 35–60 mm x 20–40 mm (Palgrave 1983), would be expected to have a lower relative frequency in the direct observation determined diet than in that determined by faecal analysis or oesophageal extrusa techniques. This effect can be seen in the results obtained from this study with the relative frequency of *R. longispina* recorded by the direct observation, oesophageal extrusa and faecal analysis techniques being 15.6%, 5.2%, and 2.2% respectively, and the relative frequency of *S. myrtina* recorded by direct observation, oesophageal extrusa, and faecal analysis techniques being 13.3%, 20.7%, and 26.2%.

A major difference between the faecal analysis technique and the other 2 techniques was that plant material underwent digestion before being collected. Two possible sources of error could have arisen from the digestive process. Firstly, epidermal particles from different species may have undergone different degrees of digestion during their passage through the gut. Secondly, epidermal fragments from different species may have had different rates of passage through the gut. The process of digestion is generally accepted as having a positive effect on the frequency of grasses and forbs, and a negative effect on the frequency of woody species (Short et al. 1974). However, several studies have shown no effect of digestion on the relative frequency of species in the faeces (Caesbeer and Koos 1970, McInnis et al. 1983). The effect of digestion on the survival of the epidermis is likely to depend on the growth stage of the plant, younger material is less likely to survive than more mature material. In the current study the frequency of grass species was probably negatively effected by digestion, as this forage class was less abundant when measured with faecal analysis than with the other 2 techniques (Table 1). The findings of the present study may reflect the maturity of the leaf material of woody plants at a time of year when no fresh growth was being produced.

The accuracy of the faecal analysis technique may also be affected by the gut transits times of different species fragments. Epidermal fragments of different species within a single faecal sample can, therefore, not be assumed to have been consumed on the same day.

All 3 techniques used in this study have inherent sources of error, and therefore no single technique can provide unequivocal measurements of diet composition. The use of direct observation without taking into account bite size is not likely to provide an accurate quantitative measure of species composition of the diet. The oesophageal extrusa technique can provide very accurate measurement of diet composition over very short sampling periods. The use of oesophageal extrusa technique to describe daily diet composition within species-rich plant communities should be based on an adequate number of daily samples in order to ensure that measure of species diversity is representative. The faecal analysis technique also has inherent errors arising from the passage of forage through the gut. The effects of digestion make it difficult to relate faecal samples to the actual time of ingestion, and variation in the survival of epidermal fragments of different species may adversely effect the accuracy of the quantitative measurement of diet composition.

Further work, using penned animals under controlled conditions, is needed to establish the number of samples required by the oesophageal extrusa technique to obtain accurate measurements of daily diet composition. Comparisons of the oesophageal extrusa, faecal analysis and direct observation also require comparison under controlled conditions where intake of each forage species can be measured, in this way the individual errors associated with each technique can be quantified and possible correction factors developed.

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Point sampling for leaf area index in sagebrush steppe communities

PATRICK E. CLARK AND MARK S. SEYFRIED

Authors are range scientist and soil scientist, USDA Agricultural Research Service, 800 Park Blvd., Plaza IV, Suite 105, Boise, Ida. 83712.

Abstract

Although point sampling has been used for more than 30 years to quantify leaf area index (LAI), this field technique has not been rigorously evaluated in sagebrush steppe plant communities. Leaf area index estimates obtained using different sampling pin inclinations or combinations of pin inclinations were evaluated in Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), low sagebrush (*Artemisia arbuscula* Nutt.), and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) communities within the Reynolds Creek Experimental Watershed near Boise, Ida. Leaf area index values determined by clipping and processing green foliage through a leaf area meter were used as evaluation standards. Pins inclined at 13° from the horizontal, used alone or in combination with pins of 52° and/or 90° inclinations, performed poorly for estimating LAI in the Wyoming big sagebrush and low sagebrush communities. Estimating total LAI with either the combination of 52° and 90° angle pins or with 52° or 90° pins alone explained at least 96% of the variability in LAI standard values from the Wyoming big sagebrush and mountain big sagebrush communities. Using 52° angle pins alone produced model fits similar to those obtained when the combination of 52° and 90° angle pins were used to estimate shrub, graminoid, and forb LAI across all 3 communities ($P > 0.1$). Collecting point data using 52° angle pins often provided better or similar model fits with LAI standards compared to other pin angles but using 90°angle pins offers a better compromise between practicality, efficiency, and accuracy.

Key Words: *Artemisia arbuscula*, *Artemisia tridentata* ssp. *vaseyana*, *Artemisia tridentata* ssp. *wyomingensis*, LAI, low sagebrush, mountain big sagebrush, Wyoming big sagebrush

Resumen

Aunque el muestreo de puntos ha sido utilizado por más de 30 años para cuantificar el índice de área foliar (IAF), esta técnica de campo no ha sido evaluada rigurosamente en las comunidades esteparias de “ Sagebrush”. Se evaluaron estimaciones del índice de área foliar obtenidas con diferentes grados de inclinación de los alfileres o combinaciones de inclinaciones en comunidades de “ Wyoming big sagebrush” (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), “Low sagebrush” (*Artemisia arbuscula* Nutt.) y “Mountain big sagebrush” (*Artemisia tridentata* Nutt. ssp. *vascyana* [Rydb.] Beetle) dentro de la Cuenca Hidrológica Experimental Reynolds Creek cerca de Boise, Idaho. Los valores del IAF determinados en forraje verde cortado y con el uso de un medidor de área foliar se utilizaron como estándares de evaluación. Los alfileres inclinados a 13 grados del plano horizontal, utilizados solos o en combinación con alfileres a 52 y/o 90 grados de inclinación, estimaron pobremente el IAF de las comunidades de “Wyoming big sagebrush” and “Low sagebrush”. La estimación del IAF total tanto con la combinación de 52 y 90 grados de ángulo de inclinación de los alfileres o con los alfileres solos a inclinados a 52 y 90 grados explicaron al menos el 96% de la variabilidad de los valores estándar del IAF de las comunidades de “ Wyoming big sagebrush” and “ Mountain big sagebrush”. Usando alfileres con una sola inclinación de 52 grados se produjeron modelos que concuerdan con los obtenidos con la combinación 52 y 90 grados de inclinación para estimar el IAF de arbustos, hierbas y gramíneas a través de las 3 comunidades ($P > 0.1$). En comparación con otros angulos de inclinacion de los alfileres, el colectar datos de punto utilizando un ángulo de inclinación de los alfileres de 52 grados a menudo provee mejores modelos o similares a los del IAF estándar, pero uso la inclinación de 90 grados ofrece un mejor balance entre lo práctico, la eficiencia y la certeza.

Point sampling has been one of the most commonly used field techniques for quantifying leaf area index (LAI) in rangelands (Bonham 1989). This technique involves pushing a sharpened pin through the vegetation canopy and recording the number of pinpoint contacts with green foliage. Leaf area index (expressed as units of green foliage surface area per unit of ground surface area) is determined by dividing the number of foliage contacts by the total number of pins used in a given area.

Other field techniques for quantifying LAI are based on light interception or destructive sampling. Where LAI is relatively low, as in the sagebrush steppe, light interception techniques overestimate LAI of woody plants because light intercepted by foliage cannot be differentiated from light intercepted by woody stems and branches (Barclay 2000). Harvesting and processing foliage through an electronic leaf area meter is the most accurate means of quantifying LAI (Beerling and Fry 1990). There are several advantages, however, in using point sampling over a leaf area meter for determination of LAI. Point sampling facilitates: 1) repeated measurement of LAI at the same sampling point over time, 2) rapid sample collection, and 3) determination of both leaf area and spatial arrangement of foliage (Warren Wilson 1963, Philip 1965).

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Typically, vertical pins (90° inclination) are used in point sampling, however, pins inclined at a shallower angle may provide more accurate estimates of leaf area index (Warren Wilson 1959, 1960, 1963). Vertical pins may underestimate LAI of grasses and other plants with erect leaves and overestimate LAI of plants with predominately horizontal leaves. Warren Wilson (1963) suggested the maximum error of point LAI estimates could be reduced to about 7% by using pins inclined at 32.5° from horizontal. Using 2 pin angles, specifically 13° and 52°, should further reduce the maximum error to 2.5%.

Although point sampling has be used for more than 30 years to quantify LAI, the technique has not been rigorously evaluated in sagebrush steppe plant communities. The objectives of this study were to evaluate different pin angles of the point sampling technique for characterizing total, shrub, graminoid, and forb LAI in 3 different sagebrush (*Artemisia* spp. Nutt.) communities.

Materials and Methods

Study Area

The study was conducted in the Reynolds Creek Experimental Watershed (RCEW) located 80 km south of Boise in southwestern Idaho (43° 11' N, 116° 46' W). The RCEW is 234 km^2 in area and ranges in elevation from 1,097 to 2,252 m. Mean annual precipitation ranges from 240 mm at lower elevations to 1,130 mm at higher elevations (Hanson et al. 1980). About 75% of the precipitation in the higher elevations falls as snow (Cooley et al. 1988). Summers are very dry throughout the watershed.

Soils of the experimental watershed are derived primarily from 4 parent materials, basalt (63% of the watershed), granite (18%), alluvium/lacustrine sediments (12%), and welded tuff (6%) (Stephenson 1977). Aridisols dominate the lowest elevations and Mollisols are most common elsewhere. Soils derived from granite are generally in coarse-loamy families and the others are generally in fine-loamy families. Excluding valley bottoms and snow drift areas, soils are shallow and rocky with steep topography.

Three sagebrush communities evaluated in this study were: 1) Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), 2) low sagebrush (*Artemisia arbuscula* Nutt.), and 3) mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle). A detailed characterization of the flora in the Reynolds Creek watershed has been conducted by Spaeth et al. (2000). The Wyoming big sagebrush community dominates at the lower elevations (< 1,400 m) of the watershed. Principal species are Wyoming big sagebrush, bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Smith), and Sandberg bluegrass (*Poa secunda* J. Presl.). The low sagebrush community occurs at the mid-elevations (1,400 to 1,600 m). Low sagebrush, Sandberg bluegrass, and arcane milkvetch (*Astragalus obscurus* S. Wats.) are the principal species in this community. The mountain big sagebrush community dominates at the higher elevations (> 1,600 m). The principal species include mountain big sagebrush, mountain snowberry (*Symphoricarpos oreophilus* Gray), mountain brome (*Bromus marginatus* Nees ex Steud.), elk sedge (*Carex geyeri* Boott), lupine (*Lupinus* spp. L), and sticky cinquefoil (*Potentilla glandulosa* Lindl.).

Sampling Procedures

Point data were collected along four or five, 30-m transects randomly located within each of the 3 sagebrush communities. Each transect was aligned north-south and contained 6 randomly selected sampling locations. A 1-m^2, square frame marked at 10-cm intervals was centered over each sampling location along a transect, forming the perimeter of the LAI sampling space for that location. A 20-pin point frame with 5-cm pin spacings, magnetic pin brakes, bubble levels, and 4 adjustable legs was straddled over the 1-m^2 frame to collect point data (Fig. 1). Although point sampling using pins grouped on a point frame is statistically less efficient than using a single, individually placed pin (Goodall 1952), point sampling to characterize LAI is most commonly done using point frames (Greig-Smith 1983). At each sampling location within the Wyoming big sagebrush and low sagebrush communities, point data were collected at 3 different pin inclination angles from the horizontal: 1)13°, 2)

Fig. 1. Sampling LAI in the mountain big sagebrush community at the Reynolds Creek Experimental Watershed near Boise, Ida. using a 20-pin frame adjusted to sample points with sharpened pins inclined 90° to the horizontal.

52°, and 3) 90°. Point data from the mountain big sagebrush community were collected using only the 52° and 90° inclinations because dense vegetation cover restricted accurate sampling at the 13° inclination.

The 90° point data for each sampling location were collected by positioning, leveling, and reading the point frame at 4 stations spaced at 20-cm intervals within the 1-m^2 frame (Fig. 1). Each of the 20 pins was pushed vertically through the plant canopy to the ground surface. All pin-point contacts with green foliage were counted, classified as either shrub, graminoid, or forb, and recorded.

The 13° and 52° point data were collected by positioning the point frame over the 1-m^2 frame, inclining the point frame to the appropriate angle, aligning the lower cross member of the point frame directly over and parallel to the edge of the 1-m^2 frame, and reading each pin. Contacts with green foliage were recorded as the pins passed from the near edge of the 1-m^2 frame, through the sampling space, and finally touched the ground surface at the opposite edge of the 1-m^2 frame. This procedure was repeated for all 4 cardinal directions at each sampling location.

This design allowed sampling of 80 points from each of the 90°, 52°, and 13° pin inclination angles from a sampling space of approximately 1 m^3 at each of the 6 locations on a transect. Transects were treated as experimental units. Point estimates of LAI were based on transect means calculated by dividing the number of contacts per transect by 480 pins per transect.

The precision and accuracy of point estimates of LAI were compared to LAI standard values determined using clipped samples and a leaf area meter. At each sampling location following completion of point sampling, ten, 1-dm^2 square frames were randomly located within the larger 1-m^2 frame. All green foliage within the vertical projection of these 10 frames was clipped, sorted, and pooled forming 1 composite sample for each of the shrub, graminoid, and forb growth forms per sampling location. To avoid leaf shrinkage and rolling, samples were stored in sealed plastic bags, refrigerated, and processed within 72 hours of harvest. Leaf area of the samples was determined using a LAI-3000 Leaf Area Meter ([1]Li-Cor, Inc., Lincoln, Nebraska) which was calibrated between runs using a standard 10-cm^2 metal disk. Note that the LAI standard values described above were estimates rather than true measurements of LAI within the 1-m^3 sampling space. True measurement of LAI required clipping all the green foliage from the entire sample space and processing this perishable material before it began to shrink and deform. Labor and equipment constraints prevented measurement of true LAI in this study.

Table 1. Observed range in total leaf area index (LAI) and percent contributions of shrub, graminoid, and forb growth forms to total LAI of Wyoming big sagebrush, low sagebrush, and mountain big sagebrush communities at the Reynolds Creek Experimental Watershed near Boise, Ida.

Community	Total LAI Range	Percent Contribution to Total LAI Shrub	Graminoid	Forb
Wyoming Big Sagebrush	0.13 – 0.34	97	3	<1
Low Sagebrush	0.03 – 0.53	76	18	6
Mountain Big Sagebrush	0.43 – 1.10	64	16	20

Statistical Analyses

The General Linear Model (GLM) procedure (SAS 1988) was used to evaluate relationships between LAI values derived from point data and LAI standard values obtained with the LAI meter in the 3 different plant communities from the shrub, graminoid, and forb growth forms. Two data sets were used in these analyses. One data set contained point data from all 3 pin angles used in the Wyoming big sagebrush and low sagebrush communities only. A step-wise regression analysis was applied to this data set to evaluate the relative contribution of 13° angle point data for estimating total LAI and shrub LAI for these 2 plant communities combined. Tests for statistical differences in the fits of the full and reduced GLM models were evaluated using extra sum of squares F-tests (Ramsey and Schafer 1997). Models with the same number of parameters (such as 13° vs. 52° angle) were compared using the adjusted coefficient of determination (adjusted R^2), root mean square error (RMSE), and slope estimates as criteria. Graminoid and forb cover were too sparse in the Wyoming big sagebrush and low sagebrush communities for an adequate evaluation of LAI.

The second data set included 52° and 90° angle point data from all 3 sagebrush communities. A step-wise regression analysis was also used to evaluate point data collected using these pin angles for estimating total, shrub, graminoid, and forb LAI for all 3 plant communities combined and of total LAI for each individual plant community. Most of the data subsets used for estimating LAI by growth form within each community exhibited highly skewed distributions preventing robust tests. Consequently, only the performance of 52° and 90° angle point data for estimating shrub and forb LAI in the mountain big sagebrush community were evaluated. Extra sum of squares F-tests were used to compare fits between full and reduced models and the adjusted R^2, RMSE, and slope estimates were used to compare models with the same number of parameters.

Results and Discussion

Range of Observed LAI

Observed total LAI values in the 3 sagebrush communities evaluated in this study were similar to those observed on the short grass steppe of Colorado (maximum LAI = 0.5, Lapitan and Parton 1996) and relatively low compared to the prairie grasslands of Kansas (maximum LAI 3.2, Welles and Norman 1991) (Table 1). Shrubs were the primary contributor to total LAI in these sagebrush communities. Graminoids made substantial contributions, however, to total LAI of the low sagebrush and mountain big sagebrush communities. Forbs made a notable LAI contribution only in the mountain big sagebrush community.

LAI Estimation with 13° Angle Pins

Point data from 13° angle pins inadequately estimated total LAI in the Wyoming big sagebrush and low sagebrush communities combined. Regressing 13° angle data against total LAI standard values produced much lower adjusted R^2 values than when 52° or 90° angle data were used (Table 2). When 13° angle data were combined with 52° and/or 90° angle data, inclusion of the 13° angle data had no effect on model fit ($P > 0.1$) except in 1 case. Using the 13° and 52° angle data combination did improve model fit over

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[1] Mention of manufactures or trade names is for the convenience of the reader only and implies no endorsement on the part of the authors or USDA.

Table 2. **Comparison of regression fit statistics revealing the contribution of point data collected using 13°, 52°, and/or 90° angle pins for estimating total and shrub leaf area index (LAI) in the combined Wyoming big sagebrush and low sagebrush communities at the Reynolds Creek Experimental Watershed near Boise, Ida.**

Regression Models[1]	Adjusted R^2	RMSE[2]
Total		
LAI = -0.0019 + 0.035(L) + 0.33(H) + 0.74(V)	0.935	0.0243
LAI = -0.00080 + 0.26(H) + 0.91(V)	0.935	0.0242
LAI = -0.0021 + 0.11(L) + 0.77(H)	0.917	0.0274
LAI = 0.0044 + 0.90(H)	0.882	0.0326
LAI = -0.00072 - 0.0033(L) + 1.2(V)	0.927	0.0257
LAI = -0.00083 + 1.2(V)	0.930	0.0252
LAI = 0.017 + 0.33(L)	0.507	0.0668
Shrub		
LAI = 0.015 - 0.061(L) + 0.62(H) + 0.37(V)	0.856	0.0357
LAI = 0.0011 + 0.59(H) + 0.38(V)	0.868	0.0341
LAI = 0.022 - 0.063(L) + 0.84(H)	0.868	0.0342
LAI = 0.0080 + 0.82(H)	0.876	0.0331
LAI = 0.0076 - 0.046(L) + 1.2(V)	0.800	0.0420
LAI = -0.0023 + 1.2(V)	0.823	0.0395
LAI = 0.13 + 0.069(L)	-0.129	0.0998

[1] Regression models where, L = 13^{o} angle pins, H = 52° angle pins, and V = 90° angle pins.
[2] RMSE = Root mean square error.

using the 52° angle data alone for estimating total LAI ($P < 0.01$).

In all cases, inclusion of 13° angle data in combination with 52° and/or 90° angle data did not affect model fit for estimating shrub LAI for the Wyoming big sagebrush and low sagebrush communities combined ($P > 0.1$) (Table 2). Additionally, there was no linear relationship between shrub LAI values estimated with 13° angle data alone and shrub LAI standard values.

The 13° inclination angle performed poorly for LAI estimation in these 2 sagebrush communities because of difficulties in sampling shrub LAI. The canopy of Wyoming big sagebrush and low sagebrush was typically elevated on a central trunk where pins inclined at 13° frequently passed under the sagebrush canopy. Only sagebrush canopy occupying the near side of the plot (where the pin first entered the plot) was sampled. Even when 13° angle pins were inserted from all 4 sides of the plot, sagebrush canopy in the plot center and elevated more than 15 cm was excluded from the sample. Since shrubs contribute most of the leaf area in Wyoming big sagebrush and low sagebrush communities (Table 1), this sampling bias produced large errors in both the shrub and total LAI estimates. Sampling several different layers of the vegetation canopy by elevating the entire point frame in a series of steps may have helped alleviate this sampling bias when 13° angle pins were used. Frame positioning and sampling using 13° angle pins in the rigid, woody canopy of these sagebrush communities was awkward and physically difficult. Consequently, improvements in LAI estimation obtained by increasing sampling intensity probably would not compensate for the greater sampling time and effort required. The 13° angle technique as applied in the current study and as described by Warren Wilson (1963) should not be used to estimate shrub or total LAI in Wyoming big sagebrush and low sagebrush communities. Because of insufficient sample size, the usefulness of the 13° angle technique for estimating graminoid and forb LAI in these 2 communities was not evaluated.

Total LAI and LAI by Growth Form for All Communities Combined

Combining 52° and 90° angle data to estimate total LAI for all 3 sagebrush communities combined resulted in a better model fit than using either 52° ($P < 0.001$) or 90° ($P < 0.001$) angle data alone (Table 3). All 3 models, however, explained more than 95% of the variability in total LAI standard values for these 3 communities.

Estimating shrub LAI for the combination of these 3 communities using either the 52° and 90° angle data combination or 52° angle data alone produced similar model fits ($P > 0.1$) with both models explaining more than 97% of the variability in shrub LAI (Table 3). Estimating shrub LAI using 90° angle data alone resulted in a poorer model fit than using the 52° and 90° angle data combination ($P < 0.05$).

Regression models based on either the combination of 52° and 90° angle data or 90° angle data alone had similar fits ($P > 0.1$) and explained more than 96% of the variability in graminoid LAI standard values (Table 3). Estimating graminoid LAI using 52° angle data alone resulted in a poorer model fit than the combination of 52° and 90° angle data ($P < 0.001$). A single outlier, representing data from a low sagebrush site located on a north slope with relatively high Idaho fescue (*Festuca idahoensis* Elmer) cover, was linked to this poor fit. With this outlier removed,

Table 3. **Comparison of regression fit statistics revealing the contribution of point data collected using 52° and/or 90° angle pins for estimating total, shrub, graminoid, and forb leaf area index (LAI) in the combined Wyoming big sagebrush, low sagebrush, and mountain big sagebrush communities at the Reynolds Creek Experimental Watershed near Boise, Ida.**

Regression Models[1]	Adjusted R^2	RMSE[2]
Total		
LAI = 0.0028 + 0.44(H) + 0.57(V)	0.973	0.0231
LAI = 0.0061 + 0.86(H)	0.959	0.0284
LAI = 0.0027 + 1.1(V)	0.959	0.0284
Shrub		
LAI = 0.0037 + 0.67(H) + 0.23(V)	0.972	0.0270
LAI = 0.0040 + 0.84(H)	0.972	0.0269
LAI = 0.011 + 1.1(V)	0.941	0.0389
Graminoid		
LAI = -0.0055 + 0.038(H) + 1.2(V)	0.965	0.0147
LAI = -0.0049 + 1.2(H)	0.836	0.0318
LAI = -0.0052 +1.2(V)	0.968	0.0141
LAI(R)[3] = -0.00059 + 1.0(H) - 0.16(V)	0.968	0.0099
LAI(R) = -0.0011 + 0.91(H)	0.968	0.0096
LAI(R) = -0.0037 +1.2(V)	0.930	0.0143
Forb		
LAI = 0.0015 + 0.92(H) + 0.076(V)	0.960	0.0180
LAI = 0.0011 + 1.0018(H)	0.963	0.0172
LAI = 0.0064 + 0.94(V)	0.939	0.0222

[1] Regression models where, H = 52° angle pins and V = 90° angle pins.
[2] RMSE = Root mean square error.
[3] LAI(R) = outlier removed.

estimating graminoid LAI using either the 52° and 90° angle data combination or 52° angle data alone resulted in similar model fits (P > 0.1) while using 90° angle data alone resulted in a poorer model fit than the 52° and 90° angle data combination (P < 0.01). The cause of this outlier is difficult to explain but may be related to potential sampling error resulting from difficulty in observing point contacts within the dense clumps of fine, rolled leaves typical of Idaho fescue.

The model fit where the 52° and 90° angle data combination was regressed against forb LAI standard values was similar to that when either 52° angle data alone (P > 0.1) or 90° angle data alone (P > 0.05) were used (Table 3). All 3 models explained more than 93% of the variability in forb LAI.

Table 4. Comparison of regression fit statistics revealing the contribution of point data collected using 52° and/or 90° angle pins for estimating total leaf area index (LAI) in the Wyoming big sagebrush, low sagebrush, and mountain big sagebrush communities and shrub and forb LAI in the mountain big sagebrush community at the Reynolds Creek Experimental Watershed near Boise, Ida.

Regression Models[1]	Adjusted R^2	RMSE[2]
Wyoming Big Sagebrush		
Total LAI = 0.0011 + 0.43(H) + 0.63(V)	0.972	0.0178
Total LAI = 0.0058 + 0.85(H)	0.964	0.0202
Total LAI = -0.0023 + 1.3(V)	0.964	0.0203
Low Sagebrush		
Total LAI = -0.0020 + 0.24(H) + 0.97(V)	0.843	0.0330
Total LAI = -0.0054 + 1.1(H)	0.732	0.0432
Total LAI = 0.0016 + 1.2(V)	0.851	0.0322
Mountain Big Sagebrush		
Total LAI = 0.0033 + 0.59(H) + 0.34(V)	0.992	0.0152
Total LAI = 0.0068 + 0.85(H)	0.986	0.0196
Total LAI = 0.0037 + 1.1(V)	0.961	0.0333
Shrub LAI = -0.012 + 0.80(H) + 0.096(V)	0.986	0.0186
Shrub LAI = -0.015 + 0.88(H)	0.990	0.0157
Shrub LAI = 0.037 + 1.0(V)	0.913	0.0460
Forb LAI = -0.0051 + 0.54(H) +0.46(V)	0.978	0.0170
Forb LAI = -0.012 + 1.0(H)	0.973	0.0187
Forb LAI = 0.0048 + 0.93(V)	0.972	0.0191

[1] Regression models where, H = 52° angle pins and V = 90° angle pins.
[2] RMSE = Root mean square error.

Total LAI and LAI by Growth Form Within Each Community

Estimating total LAI in the Wyoming big sagebrush community using either the 52° and 90° angle data combination or 52$^{\text{o}}$ or 90° angle data alone resulted in similar model fits (P > 0.05) (Table 4). All 3 models explained more than 96% of the variability in total LAI standard values.

The regression model based on the 52° and 90° angle data combination explained more than 84% of the variability in total LAI standard values from the low sagebrush community (Table 4). Estimating total LAI using the 90° angle data alone was similar to using the 52° and 90° angle data combination (P > 0.1) while using the 52° angle data produced a poorer fit than the full model (P < 0.025).

Estimating total LAI of the mountain big sagebrush community using the 52° and 90° angle data combination explained more than 99% of the variability in total LAI standard values (Table 4). Regression models based on only 52° (P < 0.01) or 90° angle data (P < 0.001) explained less of the variability in LAI standard values than the full model. Both of these reduced models, however, explained more than 96% of the variability in total LAI standard values. Although the adjusted R^2 and RMSE values in Table 4 suggest the 90° angle data did not perform as well as the full model for shrub LAI estimation, model fits using either 52° or 90° angle data alone were statistically similar to those when the 52° and 90° angle data combination was used for estimating shrub (P > 0.1) and forb (P > 0.1) LAI in the mountain sagebrush community.

The regression models described above indicate point data collected with the 90° or 52° angle pins require some correction to provide accurate estimates of LAI (Tables 3 and 4). Since the y-intercepts for each of these models did not differ from zero (P > 0.50), multiplying the point data by the regression slope value can be used to provide the correction needed to approximate the LAI standard values.

Summary and Conclusions

The 13° angle point sampling technique was difficult and impractical to apply in sagebrush communities and contained a sampling bias against shrubs. Elevating the point frame to avoid the bias by sampling multiple levels within the shrub canopy would make the technique even more difficult and impractical to apply.

Point data collected with 52° and 90° angle pins performed well for estimating LAI in the Wyoming big sagebrush, low sagebrush, and mountain big sagebrush communities. With only 2 exceptions, using the 52° or 90° angle data alone provided regression fits similar to that when the combination of 52° and 90° angle data were used (Tables 3 and 4). Even in these 2 exceptional cases (i.e., estimation of combined total LAI for all 3 communities and total LAI for the mountain big sagebrush community), improvements in the regression fit of the data obtained by applying a combination of pin angles did not offset the additional time and effort required to do so.

The 52° angle data provided a somewhat higher adjusted R^2 and lower RMSE value for modeling shrub LAI for the 3 community combination than did the 90° angle data. The 52° angle data performed as well as the 90° angle data for estimating total and forb LAI in all communities combined and total LAI in the Wyoming big sagebrush community and shrub and forb LAI in the mountain big sagebrush community.

Given the above results, the 52° angle might be considered as the technique of choice for LAI estimation in these sagebrush communities. In most cases, however, using either 52°$^{\text{o}}$ or 90° angle data explained more than 90% of the variability in the LAI standard values which would be quite satisfactory for most applications requiring LAI. Additionally, there is a trade-off between efficiency and accuracy that must be considered. Because of the obstructiveness of sagebrush steppe vegetation, inclined pins required noticeably more time and effort to position and read than 90° angle pins. Point sampling with 52° angle pins required more time to thread and align the frame legs through rigid vegetation than when 90° angle pins were sampled. Repositioning the point frame when sampling 52° angle pins also resulted in a considerable amount of inadvertent trampling outside the plot because the user was required to stand on all 4 sides of the plot while positioning the frame to sample in all 4 cardinal directions. Repositioning of the point frame for repeated sampling of 90° angle pins could be done while standing on one side of the plot thus minimizing trampling. Trampling outside the plot may eventually influence the LAI within the plot reducing the comparability of temporally-repeated LAI measurements. Furthermore, the longer pin path lengths of inclined pins resulted in noticeably more time spent waiting for pin vibrations to dampen than when 90° angle pins were used. While pin droop was not a problem when using 90° angle pins, it was a problem that had to be noted and corrected when using inclined pins. Given their practical benefits in the field, using 90° angle pins may provide a better compromise between practicality, efficiency, and accuracy than using 52° angle pins in sagebrush communities.

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Bitterbrush and cheatgrass quality on 3 southwest Idaho winter ranges

CHAD J. BISHOP, EDWARD O. GARTON, AND JAMES W. UNSWORTH

Authors are wildlife researcher, Colorado Division of Wildlife, Montrose, Colo. 81401; professor, Department of Wildlife Resources, University of Idaho, Moscow, Ida. 83844; and principal wildlife research biologist, Idaho Department of Fish and Game, Nampa, Ida. 83686. At the time of research, the senior author was research assistant, Department of Wildlife Resources, University of Idaho, Moscow, Ida.

Abstract

Nutritional stress is an important mortality factor for wintering mule deer (*Odocoileus hemionus hemionus* Rafinesque), particularly fawns. The rate at which fawns utilize existing fat stores is at least partially dependent upon the quality of available forage during winter. Although numerous studies have determined the nutritive value of various forage species, more research is needed to determine whether individual forage species vary in quality across the landscape. We determined whether differences existed in the nutritional quality of antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) and cheatgrass brome (*Bromus tectorum* L.) among 3 winter ranges and 6 habitats within the winter ranges. In vitro dry matter digestibility (IVDMD) of bitterbrush varied among winter ranges in 1996 and 1997 ($P < 0.001$). The highest mean IVDMD measured on a winter range was 29.8% ($n = 36$, SD = 3.87) in 1997 while the lowest was 15.2% ($n = 38$, SD = 4.42) in 1996. Bitterbrush crude protein (CP) was different among habitats in 1997 ($P = 0.005$), with mean CP values ranging from 7.0% ($n = 19$, SD = 0.73) to 8.0% ($n = 13$, SD = 0.70). The length and diameter of available bitterbrush leaders varied within and among winter ranges because of differential utilization. Bitterbrush IVDMD and CP varied in relation to the mean diameter of leaders obtained from each random sampling site ($P < 0.001$). The quality of bitterbrush decreased as browse intensity increased. Cheatgrass IVDMD was different between winter ranges ($P < 0.001$) in 1996, with mean values ranging from 65.8% ($n = 36$, SD = 4.34) to 69.6% ($n = 36$, SD = 3.83). Site-specific variation should be considered when evaluating the nutritional quality of mule deer habitat, at least during winter when species diversity in deer diets is limited.

Key Words: nutritional quality, mule deer, in vitro dry matter digestibility, crude protein, *Purshia tridentata*, *Bromus tectorum*

Resumen

El estrés nutricional es un factor importante de mortalidad invernal en los venados (*Odocoileus hemionus hemionus* Rafinesque), particularmente para los cervatos. La tasa a la cual los cervatos utilizan las reservas existentes de grasa es parcialmente dependiente de la calidad de forraje disponible durante el invierno. Aunque numerosos estudios han determinado el valor nutritivo de varias especies forrajeras se necesita más información para determinar si las especies forrajeras individuales varían en calidad a través del terreno. Determinamos si existen diferencias en la calidad nutricional del "Antelope bitterbrush" (*Purshia tridentata* [Pursh] DC.) y "Cheatgrass brome" (*Bromus tectorum* L.) entre 3 pastizales de invierno y 6 hábitats dentro de los pastizales de invierno. En 1996 y 1997, la digestibilidad in vitro de la materia seca (DIVMS) del "Bitterbrush" varió entre los pastizales de invierno (P < 0.001). El mayor promedio de DIVMS obtenido en un pastizal de invierno fue de 29.8% (n = 36, SD = 3.87) en 1997, mientras que el menor promedio fue 15.2% (n=38, SD = 4.42) en 1996. En 1997, la proteína cruda (PC) de "Bitterbrush" fue diferente entre hábitats (P = 0.005), con valores promedio de PC en un rango de 7.0% (n = 19, SD = 0.73) a 8.0% (n = 13, SD = 0.70). La longitud y diámetro de los tallos principales de "Bitterbrush" disponible variaron entre los pastizales de invierno debido a diferenciales de utilización. La DIVMS y PC del "Bitterbrush" variaron en relación al diámetro promedio de los tallos pincipales obtenidos de cada sitio aleatorio de muestreo (P < 0.001). La calidad del "Bitterbrsuh" disminuyó conforme la intensidad del ramoneo aumento. En 1996, la DIVMS del "Cheatgrass" fue diferente entre los pastizales de invierno (P < 0.001), con valores promedio en un rango de 65.8% (n = 36, SD = 4.34) a 69.6% (n = 36, SD = 3.83). La variación especifica por sitio debe ser considerada al evaluar la calidad nutricional del hábitat del venado, al menos durante el invierno cuando la diversidad de especies en la dieta del venado es limitada.

Winter malnutrition is a common cause of mortality for mule deer (*Odocoileus hemionus hemionus* Rafinesque) fawns, particularly during severe winters. Nutritionally stressed fawns are also more susceptible to other proximal causes of mortality. Since mule deer largely depend on pre-winter fat stores to meet energy requirements during winter, over-winter fawn survival is often determined by the duration and severity of winter (Wallmo et al. 1977, Torbit et al. 1985). Nutritional stress arises from a lack of necessary quality in forage to sustain mule deer through winter (Wallmo et al. 1977). Although nutritional maintenance requirements are rarely met, differences in the nutritive value of the forage may be very important. Deer selecting higher quality diets should deplete existing fat stores more slowly, thereby increasing the probability of survival.

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Digestibility, protein, and other indices of nutritional quality have been determined for numerous plant species eaten by mule deer (Bissell and Strong 1955, Trout and Thiessen 1973, Welch 1989, Austin et al. 1994). However, assigning a single nutritional value such as digestibility or protein to a particular forage species may not be appropriate. Relatively little research has focused on differences in quality within the same plant species. Intraspecies variation occurs as a result of genetic variability (Welch and McArthur 1979, Welch and Pederson 1981, Welch et al. 1983a, Welch 1989) and environmental factors (Laycock and Price 1970). Aside from documenting seasonal differences in quality, intraspecies variation resulting from environmental factors has been studied very little. Environmental variables which may differentially affect forage quality include temperature, precipitation/leaching, light intensity, various soil attributes, habitat type, aspect, slope, elevation, and grazing (Laycock and Price 1970). Intraspecies relationships may be particularly important in rangelands during winter, where mule deer diets comprise fewer species because the diversity of available forage is low compared to other seasons or other ecosystems.

Our goal was to evaluate intraspecies variation in nutritional quality during a short time interval (3–4 weeks) while limiting spatial variation to a portion of southwest Idaho (4950 km^2). We sampled bitterbrush (*Purshia tridentata* [Pursh] DC.) and immature, green cheatgrass (*Bromus tectorum* L.), which are both used by mule deer on southwest Idaho winter ranges. Trout and Thiessen (1973) and Scholten (1983) found that bitterbrush comprised roughly one-third of the diet of mule deer during peak winter use in southwest Idaho, indicating a strong preference when availability was considered. Scholten (Idaho Department of Fish and Game, unpublished) found that bitterbrush, on average, comprised only 15% of the available annual growth (kg ha^{-1}) of sagebrush (*Artemisia* spp. L.), bitterbrush, and rabbitbrush (*Chrysothamnus* spp. Nutt.). Austin et al. (1994) found cheatgrass to be one of several annual grasses which are nutritionally valuable to mule deer when green during the spring and fall. We determined whether differences existed in the nutritional quality of bitterbrush or cheatgrass among 3 mule deer winter ranges and among 6 habitat components in southwest Idaho, and to what extent bitterbrush quality may differ from one year to the next. We assessed nutritional quality by determining in vitro dry matter digestibility (IVDMD) and crude protein (CP).

Materials and Methods

Study Areas

Our research was conducted on 3 winter ranges in southwest Idaho. Mule deer were present on each winter range from December to early May. The Bennett Hills winter range (43°08'N 115°15'W), located 12 km north of Glenns Ferry, Ida., included the King Hill Creek and Little Canyon Creek drainages and adjacent plateaus. The area included 270 km^2 with elevations ranging from 773 m at lower King Hill Creek to 1,585 m on the upper plateaus adjacent to Little Canyon Creek. The Blacks Creek winter range (43°30'N 116°00'W) was located 15 km east of Boise, Ida., along the lower portion of the Boise River drainage. The area included 120 km^2 with elevations ranging from 950 m near Boise to 1,525 m near Three Point Mountain. The Owyhee winter range (43°10'N 116°50'W), located 45 km southwest of Boise, included the Reynolds Creek drainage. The area was 375 km^2 with elevations ranging from 750 m at lower Reynolds Creek to 1,700 m on Whiskey Mountain (Bishop 1998). Climate data for each winter range is located in Table 1.

Seven habitat components were broadly defined with 2 considerations. First, we tried to identify habitats that could be found in all 3 winter ranges. Second, we were interested in vegetation structure and cover as well as species composition. Classifications of habitat component were high shrub (> 50% shrub cover, majority of shrubs > 1 m tall), scattered high shrub (20–50% shrub cover, majority of shrubs > 1 m tall), low shrub (> 50% shrub cover, majority of shrubs <1 m tall), scattered low shrub (20–50% shrub cover, majority of shrubs <1 m tall), grass (<20% shrub cover), rock (> 70% rock cover), and riparian. In addition to bitterbrush, high shrub habitats were dominated by basin big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*) and Wyoming big sagebrush (*A. t.* ssp. *wyomingensis* Beetle and Young). Low shrub habitats primarily consisted of Wyoming big sagebrush and low sagebrush (*A. arbuscula* Nutt.). Mountain big sagebrush (*A. t.* ssp. *vaseyana* [Rydb.] Beetle) occasionally occurred in both high and low shrub habitats. Rock habitat was virtually absent from Blacks Creek. In addition to cheatgrass, grass species common among the winter ranges included wheatgrasses (*Agropyron* spp.), bluegrasses (*Poa* spp.), Idaho fescue (*Festuca idahoensis* Elmer), medusahead (*Taeniatherum caput-medusae* L.), squirrel tail (*Sitanion hystrix* [Nutt.] Smith), and Great Basin wildrye (*Elymus cinereus* Scribn. and Merr.).

Fire, Grazing, and Soils

Seventy-five percent of the Blacks Creek winter range burned in 1992. As a result, much of the area consisted of annual grassland habitats. Unburned portions of the area were used heavily by mule deer when snow prevented access to grasses, and vegetative cover was presumably necessary. No recent burns had occurred on either the Bennett or Owyhee winter ranges. All 3 winter ranges were grazed by cattle. The most intensive cattle grazing occurred on unburned private land in Blacks Creek from December through May ($\overline{x}$ = ~1.3 AUM's/ha). This private land comprised a relatively small portion of the overall winter range, but received much deer use. The remainder of the Blacks Creek range received minimal grazing. Management of grazing on the Bennett and Owyhee winter ranges was through Bureau of Land Management (BLM). The various allotments were grazed at different times and variable intensities from spring through fall, averaging approximately 0.2 AUM's/ha overall.

Table 1. Mean temperature and total precipitation obtained from weather stations in 3 mule deer winter ranges in southwest Idaho, 1995–97 (WRCC 1998).

		Mean Temperature			Total Precipitation		
Year	Season	Bennett	Blacks Cr	Owyhee	Bennett	Blacks Cr	Owyhee
			(°C)			(cm)	
1995–96	Jun.–Aug.	20.6	20.2	18.2	3.4	5.7	5.2
	Sep.–Nov.	11.6	11.2	9.9	5.7	9.3	6.1
	Dec.–-Feb.	0.5	0.5	-0.2	11.7	20.1	13.3
	Mar.–May	10.0	9.5	7.9	10.5	14.8	11.0
1996–97	Jun.–Aug.	22.2	22.1	19.5	1.1	1.1	3.3
	Sep.–Nov.	10.5	10.5	9.0	7.6	9.7	6.8
	Dec.–Feb.	1.0	0.8	1.4	16.2	27.7	18.8
	Mar.–May	10.7	10.7	9.0	4.2	9.8	8.0

The Bennett winter range was located on a mafic volcanic flow, with soils having a basaltic origin. The Blacks Creek winter range primarily contained granitic soils from a calcium-alkaline intrusive formation. The Owyhee range covered both intrusive and extrusive rock formations, with soils derived from granite, ryolite, and basalt (Johnson and Raines 1995). Soil types comprising each winter range were primarily Aridisols and Mollisols. In both the Blacks Creek and Owyhee winter ranges, 75% of the bitterbrush and cheatgrass samples were collected from Mollisols while the remaining 25% were from Aridisols (NRCS 1999a,1999c). In the Bennett winter range, 28% of samples were collected from Mollisol soils, 27% from Aridisols, 23% from rocky substrate, 16% from Vertisols, and 5% from Inceptisols (NRCS 1999b). In terms of texture, 90% of the Blacks Creek samples were from loamy soils while the remainder were from gravelly soils. In the Bennett range, 34% of sample sites comprised shallow stony loam soils, 23% comprised loamy soils, 20% sandy loam, and 23% were from rocky substrate. In the Owyhee range, 42% of sampling sites were loamy soils, 42% were shallow claypans, and 16% were sandy loams (NRCS 1999a,1999b, 1999c).

Experimental Design and Random Sampling Procedure

We collected 108 cheatgrass samples between 28 March and 26 April 1996. We collected 109 bitterbrush samples during both 1996 (20 February–13 March) and 1997 (22 February–17 March) from permanent plots. Cheatgrass sampling was not repeated in 1997 because nutritional values in 1996 were high and only minor differences due to location were observed. Intraspecific variation in cheatgrass quality would have to be large to impact mule deer survival and fitness given its high nutritional quality. Bitterbrush and cheatgrass samples were collected from 6–7 randomly selected patches of each of 6 habitat components within each winter range. Of the 7 habitat components previously defined, we did not sample bitterbrush from riparian habitat because of low prevalence, and we did not sample cheatgrass from rock habitat due to insufficient quantity. The experimental design for cheatgrass was a completely randomized design in a 3 x 6 arrangement of treatments. The experimental design for bitterbrush was a repeated measures through time in a completely randomized design with a 3 x 6 arrangement of treatments and a missing plot. The missing plot occurred because rock habitat was absent in the Blacks Creek range.

Random sampling sites were generated within each study area as latitudes and longitudes from a random numbers table and located in the field using a Garmin Global Positioning System. We collected bitterbrush and cheatgrass samples from a different winter range and multiple habitats each day so that treatments would not be confounded with any temporal variation. Within each randomly selected habitat patch, one forage sample (≥ 10 g dry weight) was collected from a 20 m radius-circular plot. We sampled most cheatgrass within the circular plot or ~10 bitterbrush plants. Each habitat patch sampled was isolated from all other patches of the same habitat component.

We recorded slope and aspect in degrees at each sampling site. Aspect values were converted to a 180° scale where northeast (45°) represented 0° and southwest (225°) represented 180°. We used ARC/INFO and ArcView software (E.S.R.I. 1996, 1997) to obtain soil and precipitation data corresponding to each site. Soil particle size and soil depth (cm) were determined from digital soil surveys (NRCS 1999a, 1999b, 1999c), and total yearly precipitation (mm) during a normal year was obtained from a digital precipitation model (Thornton et al. 1997). Soil particle size was evaluated on a continuous gradient from very fine to course particles. When sampling bitterbrush during 1996, it was visually apparent that leader length and diameter varied between sites as a result of utilization from both deer and cattle. In 1997, we recorded the mean diameter (mm) of the available leaders at each site to assess the influence of browse intensity on bitterbrush quality.

Determination of IVDMD and CP

Bitterbrush leaders and green cheatgrass were harvested by hand in a manner which simulated observed foraging behavior of mule deer (Sowell et al. 1985). Samples were air dried at a room temperature of 21°C. Dried bitterbrush samples were initially ground with a Wiley Mill using a 2 mm screen. Samples were then ground a second time using a Cyclone Mill with a 1 mm screen in place. Cheatgrass samples were ground using a coffee grinder so that minimal sample was lost during the grinding process. Ground cheatgrass comprised exceptionally fine, homogeneous particles which eliminated the need for a filter screen. Dry matter was determined by oven drying samples at 100°C (A.O.A.C. 1990). To determine IVDMD, we used the first stage of the Tilley and Terry (1963) technique as modified by Pearson (1970). The rumen inoculum source for the estimation of digestibility was obtained from Hereford-crossbred cows maintained on an alfalfa/barley diet. Welch et al. (1983b) found that different sources of rumen inocula, from both domestic and wild ruminants on different diets, similarly digested a wide variety of forages. Also, forage samples tend to be ranked correctly in terms of relative quality when different inocula sources are used (Robbins et al. 1975). Nitrogen content was analyzed by combustion using a Leco CHN 600 Analyzer. CP was determined by multiplying percent N by 6.25 (A.O.A.C. 1990).

Statistical Methods

The IVDMD and CP values were analyzed using a multivariate analysis of covariance (MANCOVA) type linear model with canonical analysis using PROC GLM in SAS (SAS Institute 1989). Winter range and habitat were the independent categorical variables, and year represented a repeated measure in the bitterbrush analysis. Covariates included Julian sampling date, slope, aspect, soil particle size, soil depth, and precipitation. Julian sampling date was selected as a covariate to determine whether nutritional quality varied temporally through the sampling period. Due to the missing cell in the experimental design for bitterbrush, Type IV sums of squares and cross products (*SS&CP*) were used. A variety of Type IV estimable functions existed for main effects and some interactions. In cases where the functions used by PROC GLM (SAS Institute 1989) excluded data, we developed meaningful functions that utilized all of the data. We then used PROC IML in SAS (SAS Institute 1995) to calculate the appropriate Type IV *SS&CP*, or hypothesis matrices. An extreme outlier in the bitterbrush data set, although biologically feasible, was removed to avoid violating the assumptions of multivariate normality and variance-covariance homogeneity.

We initially tested for differences in bitterbrush quality between winter ranges, habitats, years, and their interactions. Due to a significant winter range × year interaction, we ran separate analyses on bitterbrush quality for each year individually. For the 1997 bitterbrush data, mean leader diameter from each sampling site was included in the analysis as a covariate. For these analyses, as well as the analysis of cheatgrass quality, we tested for differences between winter ranges and habitats and the interaction. We were unable to test for differences between habitats within each winter range due to insufficient sample size and therefore low power. We used Wilks' lambda as the test statistic for all analyses, which was converted to an F statistic to evaluate significance. Each of the commonly used multivariate test statistics gave similar results. For each significant result, we proceeded with a canonical analysis. A canonical variable is a combination of dependent variables which explain variation among data points. The first canonical variable accounts for the greatest amount of variation in the data set, followed by the second canonical variable and so forth. Canonical variates were assessed by looking at both the standardized canonical coefficients and the within canonical structure (SAS Institute 1989). Analyses of covariance (ANCOVA) were performed on IVDMD and CP individually for any significant tests obtained from the MANCOVA. Tukey's studentized range test (HSD) was used to make pairwise mean comparisons of significant main effects obtained from the ANCOVA's.

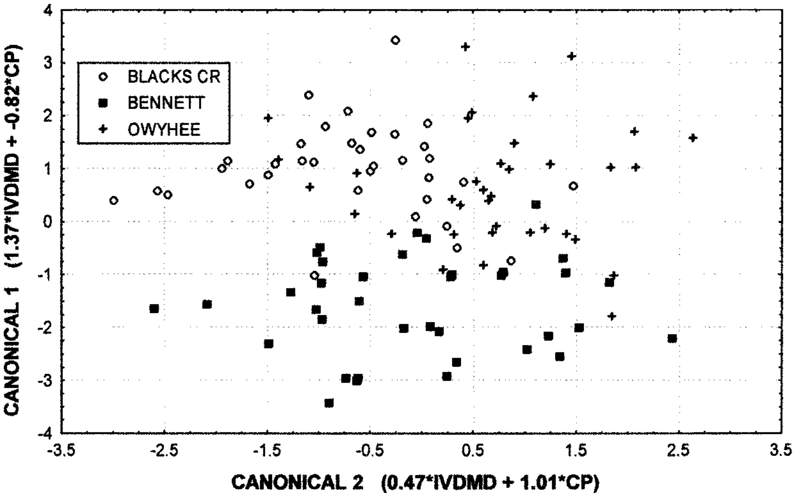

Fig. 1. Canonical plot of bitterbrush quality in relation to 3 mule deer winter ranges in southwest Idaho, 1996. Canonical 1 is the combination of in vitro dry matter digestibility (IVDMD) and crude protein (CP) that explains the most bitterbrush variation among winter ranges. The Blacks Creek and Owyhee ranges are distinguished from the Bennett range along this axis due mostly to IVDMD differences. Canonical 2 is the combination of IVDMD and CP that explains the next most variation among winter ranges. The Owyhee range is separated from Blacks Creek along this second axis due primarily to CP differences. The 2 canonical variables together distinguish each study area from the other.

Results

Bitterbrush Quality

Bitterbrush quality, evaluated in terms of IVDMD and CP, varied between winter ranges ($P < 0.001$) and years ($P < 0.001$) and there was a range × year interaction ($P < 0.001$). The first canonical variate for the interaction explained 99.9% of the variation in the eigenvalue structure, and was therefore the only canonical variable of interest. In vitro dry matter digestibility was the most important variable in describing canonical 1. Bitterbrush digestibility substantially increased from 1996 to 1997 in the Bennett and Owyhee winter ranges but slightly decreased in Blacks Creek. The main effect of habitat was not significant, nor were the range × habitat, habitat × year, and range × habitat × year interactions ($P > 0.10$).

In 1996, bitterbrush quality varied between winter ranges ($P < 0.001$) but not habitats ($P = 0.057$), and the range x habitat interaction was not significant ($P = 0.878$). Precipitation ($P = 0.051$) and soil depth ($P = 0.061$) effectively explained variation in the data and improved tests of the main effects. Sampling date ($P = 0.938$), aspect ($P = 0.645$), slope ($P = 0.262$), and soil particle size ($P = 0.774$) were ineffective covariates and therefore removed from the analysis. Canonical 1 for winter ranges explained 84% of the variation in the eigenvalue structure, while the second canonical accounted for the remaining 16% of the variation. Both canonical variates were significant ($P < 0.001$). In vitro dry matter digestibility was the most influential variable in canonical 1 (1.37*IVDMD + –0.82*CP), which distinguished the Bennett range from the Blacks Creek and Owyhee ranges. Crude protein explained the most variation in canonical 2 (0.47*IVDMD + 1.01*CP), which distinguished Blacks Creek from the Owyhee range (Fig. 1). For IVDMD, each of the 3 winter ranges were different from one another with $\alpha = 0.05$. Bitterbrush in the Owyhee winter range had the highest mean digestibility followed by Blacks Creek, while the Bennett range had the lowest mean digestibility. For CP, the Blacks Creek range was significantly lower than both the Bennett and Owyhee ranges, which were not significantly different (Table 2).

In 1997, mean leader diameter of bitterbrush from each sampling site was included in the analysis as a covariate. In 1997, bitterbrush quality varied between winter

Table 2. In vitro dry matter digestibility (IVDMD) and crude protein of bitterbrush for 3 mule deer winter ranges and 6 habitat components in southwest Idaho, 1996–97.

		IVDMD				Crude Protein			
		1996		1997		1996		1997	
Treatment	Class	$\bar{x}^1$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
		(%)				(%)			
Winter Range	Bennett	15.2^{a}	4.42	23.2^{b}	4.74	7.3^{b}	0.59	7.3	0.76
	Blacks Creek	21.9^{b}	3.74	20.4^{a}	4.76	6.5^{a}	0.53	7.2	0.67
	Owyhee	24.6^{c}	4.42	29.8^{c}	3.87	7.2^{b}	0.54	7.5	0.71
Habitat	High Shrub	21.7	5.41	24.6	5.11	7.1	0.60	7.1^{a}	0.59
	Low Shrub	20.1	5.43	24.8	6.44	6.8	0.66	7.3^{a}	0.74
	Scattered High Shrub	20.8	5.49	24.0	6.90	7.2	0.70	7.4^{ab}	0.71
	Scattered Low Shrub	19.1	6.59	23.6	4.81	6.7	0.71	7.0^{a}	0.73
	Grass	20.3	4.87	24.4	6.65	7.0	0.60	7.3^{a}	0.67
	Rock	20.8	7.62	26.5	5.17	7.4	0.42	8.0^{b}	0.70
Overall	Total Sample	20.5	5.78	24.5	5.85	7.0	0.66	7.3	0.72

[1] Within columns for each treatment, means with the same letter are not significantly different ($P > 0.05$). Letter superscripts are included only where post hoc mean comparisons were warranted.

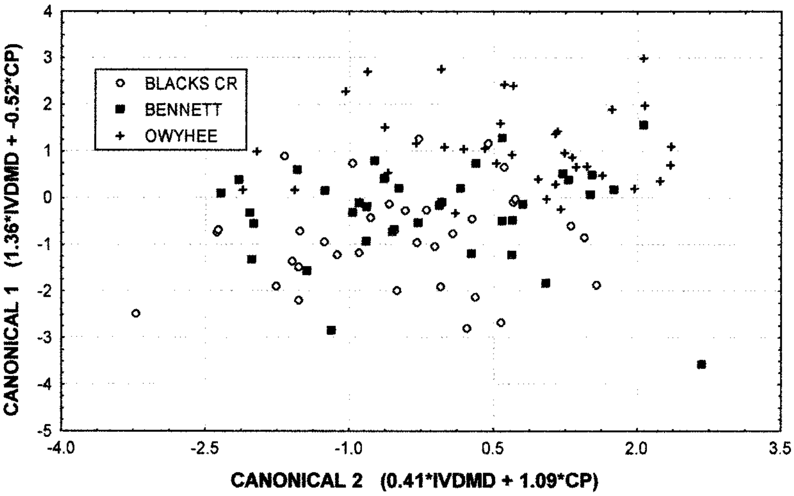

Fig. 2. Canonical plot of bitterbrush quality in relation to 3 mule deer winter ranges in southwest Idaho, 1997. Canonical 1 is the combination of in vitro dry matter digestibility (IVDMD) and crude protein (CP) that explains the most bitterbrush variation among winter ranges. The 3 ranges are reasonably separated along the canonical 1 axis as a result of IVDMD differences. The canonical 2 axis, driven by CP, does not provide any separation of the winter ranges, indicating that CP differences were minor.

ranges ($P < 0.001$) and habitats ($P = 0.035$), and the range × habitat interaction was not significant ($P = 0.342$). Bitterbrush leader diameter was significant ($P < 0.001$), indicating that utilization of leaders by deer and cattle influenced quality. Sampling date ($P = 0.403$), soil particle size ($P = 0.370$), soil depth ($P = 0.370$), precipitation ($P = 0.841$), aspect ($P = 0.585$), and slope ($P = 0.286$) did not explain variation in the data and were removed from the analysis. Canonical 1 for study areas accounted for 94% of the variation in the eigenvalue structure and was the only significant canonical. The IVDMD was the most important variable for explaining variation in canonical 1 ($1.36*IVDMD + –0.52*CP$), which distinguished each winter range from the others (Fig. 2). Canonical 1 for habitats ($–0.10*IVDMD + 1.20*CP$) explained 94% of the variation in the data, but CP was the most important variable. Thus, winter ranges varied as a result of differences in digestibility while habitats varied in response to protein differences. Each of the winter ranges were different from one another in terms of IVDMD. Bitterbrush from the Owyhee range had the greatest digestibility followed by the Bennett range, while that from Blacks Creek had the least digestibility. For habitat differences in CP, rock was greater than all other habitats except scattered high shrub, which was not significantly different from any other habitat (Table 2). For the leader diameter covariate, both IVDMD and CP were important in explaining the single canonical variable. As leader diameter of bitterbrush increased, both IVDMD and CP decreased ($P < 0.001$) (Fig. 3). Differences in leader diameter were a function of browse intensity, indicating that bitterbrush quality decreased as leader utilization increased.

Cheatgrass Quality

Cheatgrass was sampled only during 1996. Cheatgrass quality varied between winter ranges ($P = 0.002$) but not habitats ($P = 0.298$), and the range × habitat interaction was not significant ($P = 0.661$). Sampling date was not significant ($P = 0.947$); as with bitterbrush, cheatgrass quality did not vary temporally during our sampling period. Soil particle size ($P = 0.680$), soil depth ($P = 0.700$), and precipitation ($P = 0.200$) did not account for variation in the data and were removed from the analysis. Both aspect ($P = 0.075$) and slope ($P = 0.096$) were effective covariates by describing variation in the model and were retained in the analysis. Canonical 1 for winter ranges, driven by IVDMD, described 97% of the variation in the eigenvalue structure and was the only significant canonical. For IVDMD, cheatgrass in the Owyhee range had significantly higher digestibility than either the Bennett or Blacks Creek ranges, which were not different. Cheatgrass CP was virtually the same for the 3 winter ranges (Table 3).

Discussion

Bitterbrush Quality

Ammann et al. (1973) estimated that diets with 50% digestibility would meet the minimum maintenance requirement for a deer. Our estimates of bitterbrush IVDMD were considerably lower than 50% in all cases. This was expected based on previous winter estimates of bitterbrush IVDMD, which have ranged from 16.3 to 33.2% (Ward 1971, Urness et al. 1977, Welch and Pederson 1981, Welch et al. 1983a, 1983b, Welch and Wagstaff 1992). Our estimates of bitterbrush CP met the

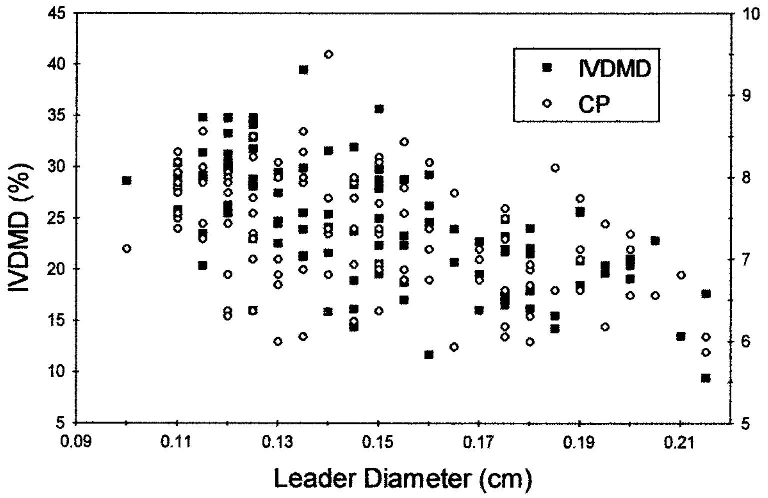

Fig. 3. Bitterbrush in vitro dry matter digestibility (IVDMD) and crude protein (CP) as a function of the diameter of available leaders among 3 mule deer winter ranges in southwest Idaho, 1997.

Table 3. In vitro dry matter digestibility (IVDMD) and crude protein of cheatgrass for 3 mule deer winter ranges and 6 habitat components in southwest Idaho, 1996.

		IVDMD		Crude Protein	
Treatment	Class	$\bar{x}^1$	SD	$\bar{x}$	SD
		------ (%) ------		------ (%) ------	
Winter Range	Bennett	67.3^a	3.81	18.4	3.12
	Blacks Creek	65.8^a	4.34	18.6	2.40
	Owyhee	69.6^b	3.83	18.9	2.60
Habitat	High Shrub	67.0	5.00	18.9	3.10
	Low Shrub	67.0	2.78	17.3	2.30
	Scattered High Shrub	66.3	5.55	18.6	2.26
	Scattered Low Shrub	67.9	3.54	18.9	3.17
	Grass	68.0	4.25	19.2	3.31
	Riparian	69.3	3.81	18.6	1.64
Overall	Total Sample	67.6	4.27	18.6	2.70

[1] Within columns for each treatment, means with the same letter are not significantly different ($P > 0.05$). Letter superscripts are included only where post hoc mean comparisons were warranted.

approximate 5–7% minimum CP requirement for deer maintenance (Einarson 1946, Dietz 1965, Murphy and Coates 1966, Holter et al. 1979). Again, this was expected based on previous winter estimates of bitterbrush CP, which have ranged from 5.9 to 9.9% throughout the western U.S. (Bissell and Strong 1955, Dietz et al. 1962, Trout and Thiessen 1973, Tueller 1979). Although bitterbrush does not appear to meet the demands of mule deer, particularly in terms of digestibility, most available forage during the winter is nutritionally poor. In general, bitterbrush is considered an important shrub to wintering mule deer based on its palatability, ubiquity, relative quality, lack of essential oils (monoterpenoids), and the low availability of green forbs and grasses.

We found that bitterbrush quality, particularly IVDMD, varied among several deer winter ranges in southwest Idaho, and that quality decreased with increased utilization by deer and cattle. The Owyhee winter range had the highest bitterbrush quality both years. Of the 3 areas, it by far had the lowest mean deer density (1.3 ± 0.1 deer km$^{2\ -1}$). Conversely, the Bennett and Blacks Creek ranges had significantly lower overall quality yet supported greater mean deer densities (7.7 ± 0.2 deer km$^{2-1}$ and 9.0 ± 0.4 deer km$^{2-1}$, respectively). The reported densities represent means for the entire winter ranges; deer densities in portions of the winter ranges were considerably higher. In 1997, we observed the least utilization on bitterbrush shrubs in the Owyhees, followed by the Bennetts, with the most utilization observed in Blacks Creek. This was consistent with the mean diameter of available leaders for each winter range, which was inversely related to bitterbrush quality (Fig. 4).

Given the low availability of shrub habitats across the Blacks Creek winter range, deer use of shrubs was heavily concentrated. We documented intense use of bitterbrush by measuring the diameter of available leaders. Large leader diameters, as a result of utilization, were directly correlated with poor bitterbrush quality in the Blacks Creek range (Fig. 4). The range fire in Blacks Creek not only reduced the quantity of shrubs, but also the quality (of bitterbrush) by concentrating use. During the 1996–97 winter, which is when we recorded leader diameters, weather conditions were average. In exceptionally harsh winters, deer have a greater reliance on shrubs, and the potential exists for extremely high deer mortality due to malnutrition, particularly for fawns. Similarly, fall drought conditions limiting growth of grasses may lead to high mortality when shrub cover is limited (Short 1981, Austin and Urness 1983, Urness et al. 1983).

The variation we observed in bitterbrush quality may be important for determining the nutritional quality of mule deer diets during winter. This is particularly true in southwest Idaho, where the variety of available forage is limited. In the Owyhee Mountains, 55 km south of our study area, Trout and Thiessen (1973) found that 97% of the February diets of mule deer consisted of bitterbrush, western juniper (*Juniperus scopulorum* Sarg.), and sagebrush. Given such low species diversity, site-specific variation in the nutritional quality of a single species could account for differences in diet quality among individual deer which seemingly do not exist based on the species composition of their diets.

Habitat explained some differences in bitterbrush CP, while precipitation, soil, and terrain variables accounted for minimal or no variation in bitterbrush IVDMD and CP. These factors likely contribute to regional differences in bitterbrush quality (i.e. one state to the next), where differences among various environmental variables are more pronounced. Genetic variation in bitterbrush likely exists at larger spatial scales as well (Welch et al. 1983a), probably as a result of differing climatic conditions and soil properties. Excluding differential browsing effects, intraspecies variation was apparently minor within the limited geographical extent of the deer winter ranges studied.

Cheatgrass Quality

Our estimates of cheatgrass IVDMD, which ranged from 65.8 to 69.6% across the winter ranges, were much greater than

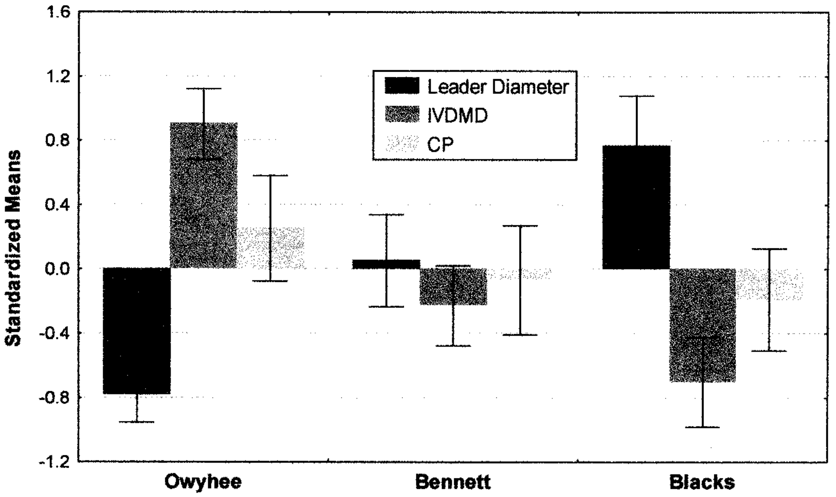

Fig. 4. Relative differences in bitterbrush leader diameter, in vitro dry matter digestibility (IVDMD), and crude protein (CP) among 3 mule deer winter ranges in southwest Idaho, 1997. The 95% confidence interval is shown for each standardized mean estimate.

the 50% minimum digestibility requirement for deer maintenance (Ammann et al. 1973). Austin et al. (1994) estimated cheatgrass in Utah to have 72.2% digestible dry matter. Given the high nutritional value of immature green grasses in general, the differences we found in cheatgrass digestibility probably have little biological relevance for mule deer. Our estimates of cheatgrass CP were nearly identical across the 3 winter ranges, which had a mean of 18.6%. A diet containing 16-17% CP is thought to meet the maximum needs of mule deer (Verme and Ullrey 1972). Previous protein estimates of green cheatgrass have ranged from 21.2% (Austin et al. 1994) to 25.6% (Dietz et al. 1962). Our nutritive values for cheatgrass verify the importance of green grass to wintering mule deer in southwest Idaho. Austin et al. (1994) evaluated the nutritional quality of 16 grasses found on deer winter ranges, all of which met or exceeded the nutritional requirements of deer. The timing and accessibility of green-up appears to be more critical for mule deer condition and survival than selection for particular grasses.

Conclusions

Future research evaluating mule deer habitat in terms of nutritional quality should consider site-specific nutritional variation within a single species along with interspecies differences, at least during winter when species diversity is limited. In our study, browsing pressure appeared to be the most important cause for observed differences in the nutritional quality of bitterbrush. Bitterbrush was the most nutritious in the Owyhee range, which had a low deer density. Higher deer densities coupled with fairly intense livestock grazing in places apparently reduced the quality of bitterbrush in the Blacks Creek and Bennett ranges. To improve habitat quality for deer in these and similar winter ranges, actions should be taken to promote shrub productivity and vigor while preventing excessive utilization of browse species prior to winter. Such actions include reseeding following natural or prescribed fire where appropriate shrub species are included in the seed mixture, and carefully managing the timing and intensity of grazing on winter range habitat.

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Redberry juniper canopy cover dynamics on western Texas rangelands

DARRELL N. UECKERT, ROBERT A. PHILLIPS, JOSEPH L. PETERSEN, X. BEN WU, AND DANIEL F. WALDRON

Authors are professor, former graduate research assistant, and senior research associate, Texas Agricultural Experiment Station, 7887 U.S. Hwy. 87 North, San Angelo, Tex. 76901-9714, assistant professor, Rangeland Ecology & Management Department, Texas A&M University, College Station, Tex. 77843-2126, and associate professor, Texas Agricultural Experiment Station, San Angelo, Tex. 76901-9714.

Abstract

Knowledge of the rate woody plant canopy cover increases is essential for understanding the ecology of rangeland plant communities, determining the economic feasibility of brush management practices, and for scheduling initial and maintenance control practices. We determined rates of change in redberry juniper (*Juniperus pinchotii* Sudw.) canopy cover from the mid 1950s through the late 1990s at 5 locations in western Texas on rangeland that had been chained or grubbed for juniper control and on adjacent untreated areas. Juniper cover was estimated from aerial photographs by the line intercept method using a 10-X monocular lens with a vernier. Juniper cover increased at 0.35 ± 0.06 percentage units year^{-1} on untreated sites and at 1.01 ± 0.07 percentage units year^{-1} following chaining or grubbing. Juniper cover returned to pre-treatment levels in an average of 20 years (range 11 to 25) following chaining or grubbing. Herbage production on untreated rangeland was predicted to decline slowly (2.4 to 5.0 kg ha^{-1} year^{-1}) as juniper cover increased from 6 to 14% and rapidly (> 8 kg ha^{-1} year^{-1}) as juniper cover increased from 30 to 38%. Herbage production was predicted to decline at a constantly increasing rate following mechanical control of juniper, from < 2 kg ha^{-1} year^{-1} in year 1 to 23 kg ha^{-1} year^{-1} in year 29. Potential additional livestock carrying capacity due to juniper control would be under estimated by more than 40%, assuming forage production without treatment remained constant during the entire planning horizon of an economic analysis. To avoid significant reductions in livestock carrying capacity, redberry juniper control should be implemented before its canopy cover exceeds about 20%.

Key Words: *Juniperus pinchotii*, mechanical brush control, aerial photography, line transects, juniper management, herbage production

Resumen

Conocer la tasa de incremento de la cobertura de copa de las plantas leñosas es esencial para entender la ecología de las comunidades vegetales de pastizal, determinar la factibilidad económica de las prácticas de manejo de arbustos y para programar las prácticas de control inicial y de mantenimiento. En 5 localidades del oeste de Texas determinamos las tasas de cambio de la cobertura de copa del "Redberry juniper" (*Juniperus pinchotii* Sudw.) ocurridas de mediados de la década de los 50's a finales de la década de los 90's. Las determinaciones se llevaron a cabo en un pastizal en el que el "Juniper" se controlo con cadeneo y extracción y en áreas adyacentes sin control de "Juniper". La cobertura de "Juniper se estimó de fotografías aéreas con el método de línea de intercepción utilizando un lente monocular de 10X con un vernier. En los sitios no tratados la cobertura de "Juniper" aumentó en 0.35 ± 0.06 porcentaje unidades año-$^{-1}$ y en 1.01 ± 0.07 porcentaje unidades año^{-1} después del cadeneo o extracción. La cobertura de "Juniper regresó a los niveles de pre-tratamiento en un promedio de 20 años (rango de 11 a 25) después del cadeneo o extracción. En los pastizales si tratamiento se predijo un disminución lenta de la producción de forraje (2.4 a 5.0 kg ha^{-1} año^{-1}) conforme la cobertura de "Juniper" aumentó de 6 a 14% y una disminución rápida (> 8 kg ha^{-1} año^{-1}) conforme la cobertura de "Juniper" aumentó de 30 to 38%. Se predijo que la producción de forraje disminuira a una tasa constantemente mayor después del control mecánico del "Juniper", de < 2 kg año^{-1} en el año 1 a 23 kg año^{-1} en el año 29. La capacidad de carga animal potencial adicional debida al control de "Juniper"sería subestimada por mas de 40%, asumiendo que la producción de forraje sin control permaneció constante durante el horizonte de planeación completo de un análisis económico. Para evitar reducciones significativas en al capacidad de carga animal el control de "Redberry juniper"debe ser implementado antes de que su cobertura de copa exceda el 20%.

Redberry juniper (*Juniperus pinchotii* Sudw.) is a basal-sprouting conifer that usually has several stems arising from the base. It is believed to be a stabilized hybrid of alligator juniper (*J. deppeana* Steud.) and one-seed juniper [*J. monosperma* (Engelm.) Sarg.] that developed during the Pleistocene era (Hall and Carr 1968). Redberry juniper occurs in southwestern Oklahoma, western Texas, southeastern New Mexico, southern Arizona, and northeastern Mexico (Correll and Johnston 1970). Prior to development of the rangeland livestock industry, redberry juniper was primarily restricted to rocky outcrops and rocky, north-facing slopes where it was protected from intense grass fires (Ellis and Schuster 1968). Since the late 1800s, redberry juniper woodlands have rapidly spread and thickened on adjacent slopes and grasslands. A 1982 survey indicated that this species occurred on about 4.7 million ha of rangeland in Texas (Soil Conservation Service 1985). Redberry juniper infestations increased by about 60% (1.5 million ha) during the period 1948 to 1982 in a 65-county region in northwestern Texas (Ansley et al. 1995).

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Excessive cover of redberry juniper is detrimental to rangeland livestock production, wildlife habitat quality, and rangeland watersheds. Herbaceous production declines as juniper canopy cover increases and as the plants mature (McPherson and Wright 1990a, Dye et al. 1995, Johnson et al. 1999). Only about 34% of annual rainfall reaches mineral soil beneath redberry junipers in western Texas because of interception by the canopy and litter layers (Thurow and Hester 1997).

Knowledge of the rate redberry juniper canopy cover increases is critical to better understanding its ecology, scheduling initial and maintenance control practices, and for assessing the economic feasibility of alternative control practices. Two relationships between woody plant canopy cover and time are important in economic analysis. First, the rate woody plant cover increases subsequent to a control practice determines the effective treatment life, which is defined as the length of time (years) for forage production to return to pretreatment levels (Conner 1985). Second, knowledge of the rate woody plant cover increases without treatment and subsequent to treatment is necessary to estimate additional herbage production due to treatment (Johnson et al. 1999). Two-way chaining followed by periodic prescribed burning was recently shown to be economically feasible for redberry juniper control (Johnson et al. 1999), but field data were not available on the rate of increase in juniper cover. Objective 1 of this study was to determine the rates of increase in redberry juniper canopy cover on untreated and mechanically treated rangeland in western Texas. Our hypothesis was that juniper cover increased faster following mechanical control than on untreated rangeland. This hypothesis was based on personal observations by the senior author of dozens of sites in the Edwards Plateau region of Texas where redberry juniper had been mechanically controlled. Objective 2 was to apply the knowledge gained in objective 1 to estimate the temporal effects of changes in redberry juniper cover on herbage production and livestock carrying capacity during the conversion of grasslands or juniper savannas to juniper woodlands.

Materials and Methods

Study Sites

Redberry juniper woodlands were studied at 5 locations across the northern and western Edwards Plateau region of Texas (Fig. 1) along an average annual rainfall gradient from 46 to 62 cm. Two, 16.2-ha sites were selected at each location, 1 with and 1 without a history of mechanical control. The 2 sites were in close proximity, on similar soils, and were situated where man-made or topographical features facilitated locating the sites on large-scale aerial photographs. The study sites were selected where: (1) redberry juniper was the dominant overstory species and juniper cover was heavy; (2) no other large, evergreen woody species were present that could be mistaken for junipers on aerial photographs taken during winter; (3) maintenance juniper control treatments had not been applied subsequent to the initial mechanical control treatments; and (4) past grazing management was typical for the region.

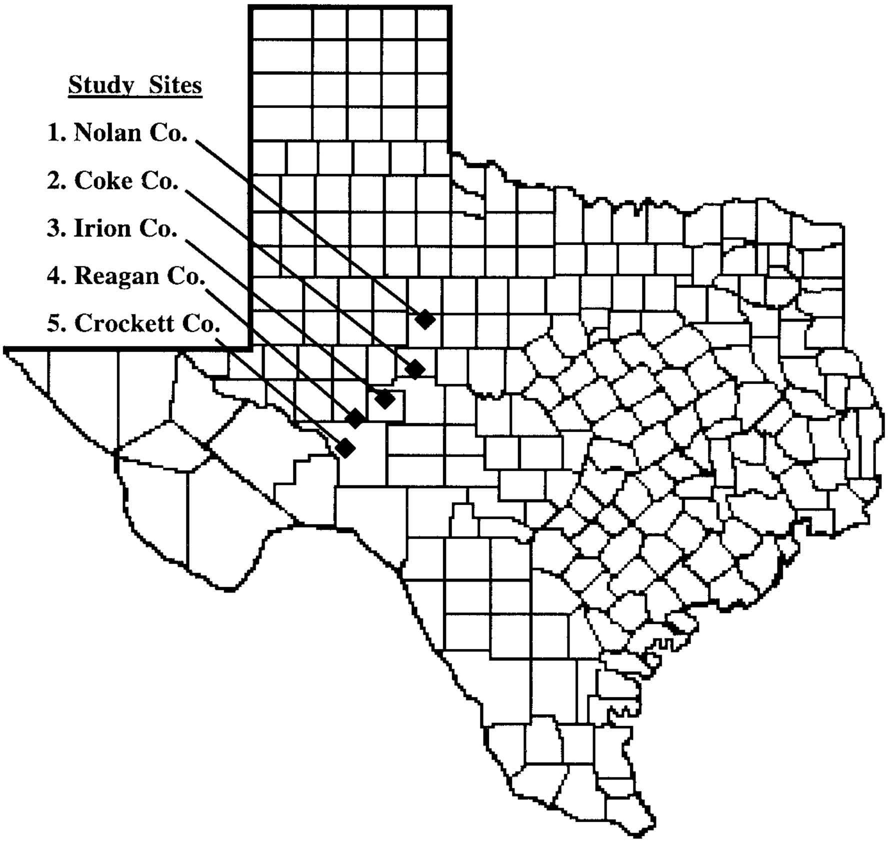

Fig. 1. Locations of redberry juniper study sites in the Edwards Plateau, Tex.

Positive transparencies of all available aerial photographs (nominal scale 1:7,900) of each site were purchased from the USDA Farm Services Agency Aerial Photography Field Office in Salt Lake City, Utah. All photographs were taken during winter and redberry juniper plants or clusters were evident as dark patches within the grey matrix of dormant grasses and bare ground. Aerial photographs were taken in 1957, 1964, 1973, 1985, and 1996 for Coke County; 1963, 1985, and 1996 for Crockett County; 1955, 1964, 1977, 1985, and 1996 for Irion County; 1957, 1964, 1976, 1985, and 1996 for Nolan County; and 1961, 1985, and 1996 for Reagan County. Photographs for Coke County, undisturbed-1985; Irion County, mechanically controlled-1985; and Nolan County, undisturbed-1976 and mechanically controlled-1985 were not used because juniper canopies could not be readily distinguished.

Descriptions of the study sites and juniper control treatments are given in Table 1. The soils at all sites were shallow with rapid surface runoff and low to very low water-holding capacity. Information about the soils was obtained from Barnhill (1974), Lowther (1981), Wiedenfeld (1986), C.C. Wiedenfeld (unpublished), and R. Dowell (unpublished).

Estimating Redberry Juniper Canopy Cover

Large-scale aerial photography has been effectively used for quantifying changes in woody plant canopy cover (Archer et al. 1988, Knapp et al. 1990, Soulé and Knapp

Table 1. Study locations where redberry juniper canopy cover was estimated from aerial photographs.

County	Avg. Rainfall[1] (cm yr^{-1})	Treatment	N Lat	W Long	Range Site	Soil
Coke	58.7	None and chained 2 ways in 1970	31° 43'	100° 32'	Low stony hill	Tarrant association[2] (shallow clays mixed with stones)
Crockett	46.0	None and chained 1 way in 1971	30° 40’	101° 33'	Limestone hill	Noelke-Ozona-Crocko complex[3] (shallow silty clay loams containing many limestone fragments)
Irion	49.2	None and chained 2 ways in 1972	31° 23'	100° 48'	Limestone hill	Ector series[4] (shallow, loamy, very gravelly, very stoney)
Nolan	62.2	None and grubbed in 1976	32° 24' 32° 24'	100° 20' 100° 17'	Loamy prairie	Quinlan loams[5] (shallow, loamy soils on uplands)
Reagan	46.8	None and chained 2 ways in 1978	31° 05'	101° 28'	Limestone hill	Noelke series[6] (shallow, very cobbly, silty clay loams)

[1] Average annual rainfall for the period covered by aerial photographs for the respective sites.
[2] Tarrant soils are clayey-skeletal, montmorillonitic, thermic, Lithic Haplustolls.
[3] Noelke-Ozona soils are loamy-skeletal, mixed superactive, thermic Lithic Petrocalcic Calciustolls: Crocko soils are fine, smectitic, thermic Vertic Calciustolls.
[4] Ector soils are loamy-skeletal, carbonatic, thermic Lithic Calciustolls.
[5] Quinlan loams are loamy, mixed, thermic, shallow Typic Ustochrepts.
[6] Noelke soils are loamy-skeletal, mixed, thermic, shallow Petrocalcic Calciustolls.

1999, Wu et al. 2000, Ansley et al. 2001). In this study, a 10-X hand lens with a vernier was used to estimate juniper cover by the line intercept method (Bonham 1989) on each 16.2-ha plot on the aerial photographs. Aerial photographs were placed on a light table during sampling. The center one hundred, 0.1-mm increments of the vernier were used for line transects. The ground scale of a transect was 79 m with observations at a scale of 0.79 m on the earth’s surface. Forty-five line transects were sampled per plot for each date. The mean canopy cover was calculated for each plot for each date.

Data Analysis

The rate of change in redberry juniper canopy cover (percentage units year $^{-1}$) for each plot was calculated by dividing the percentage point change in cover from photograph A to photograph B (e.g., from 1957 to 1964) by the number of years that had lapsed between the 2 photographs. Live juniper cover remaining subsequent to application of mechanical control practices was assumed to be about 1% based on our observations of commercial chaining and grubbing operations in western Texas.

An aerial photograph within a year prior to application of the mechanical control treatment was available for only 1 of the treated sites. Juniper canopy cover prior to treatment for the other 4 treated sites was estimated using earlier pre-treatment canopy cover estimates and the pre-treatment rate of change for the plot. If too few pre-treatment photographs were available for determining pre-treatment rate of cover change, then the rate of cover change for the pre-treatment period from the undisturbed plot at the same location was used for the calculation.

Regression was used to estimate the rate of increase in juniper cover. Data from all untreated sites were analyzed using a general linear (PROC GLM, SAS 1989) model that contained a fixed effect for site and a linear regression coefficient for year. A separate analysis was conducted for treated sites using the same model except that the year of treatment was set to zero and all other years were expressed as the number of years post-treatment.

Analysis of variance was used to test for differences in rates of change in redberry juniper canopy cover from the time of treatment to the latest aerial photograph on chained or grubbed plots and for this same time interval on untreated plots. Locations (n = 5) were utilized as replications in this analysis.

Regression analysis was used to test for relationships between rates of juniper canopy cover change and average annual precipitation, median annual precipitation, and initial juniper cover. Precipitation data were from the weather station nearest to each study site (National Oceanic and Atmospheric Administration 1998).

Yearly redberry juniper canopy cover values were calculated for untreated rangeland (range 6 to 46%) and subsequent to chaining or grubbing (range 1 to 30%) using the respective estimates for the annual rates of cover change. These yearly juniper cover values were then used as the independent variable (X) in the natural log model of the relationship between annual herbage production (Y) and redberry juniper canopy cover (X) developed by Johnson et al. (1999) to estimate the decline in total herbaceous production as a function of time. The Johnson et al. (1999) production function is defined as:

$$Y = e^{7.1626024 - 0.000441X^2}, \qquad \textbf{(1)}$$

where Y = annual herbage production (kg ha^{-1}), X = redberry juniper canopy cover (%), and e = 2.718282 (r^2 = 0.9054). Regression models were fitted to the data to quantify the change of annual herbage production as a function of time.

The Johnson (1999) natural log model and our estimates of the rates of increase in juniper cover were also used to estimate the impact of redberry juniper control on livestock carrying capacity. Analyses were conducted for pre-treatment juniper canopy cover values of 20 and 30%. In these analyses, we assumed herbage production would reach maximum values in the second growing season following juniper control (Dye et al. 1995). We also assumed a 25% harvest efficiency for proper use (White and McGinty 1992) and that an animal unit (A.U.) consumed 11.8 kg of forage day^{-1} or 4,308 kg of forage year^{-1} (oven-dry basis) (Range Term Glossary Committee 1974). Carrying capacity was calculated as animal unit years (A.U.Y.) section^{-1} (259 ha). Treatment life (TL_1) was assumed to be the length of time (years) following treatment for carrying capacity to return to the pre-treatment level, and TL_2 was the length of time (years) following treatment for carrying capacity to equilibrate with that which would have occurred in the absence of juniper control. Additional carrying capacity values, ACC_1 and ACC_2, were calculated as the difference between carrying capacity with and without juniper treatment for TL_1 and TL_2, respectively.

Results and Discussion

Changes in Juniper Canopy Cover
Untreated Rangeland

Juniper canopy cover in the earliest aerial photographs of plots that were not treated ranged from 6 (Crockett County) to 33% (Irion County) (Fig. 2). These differences appeared to influence the rate of change in cover for 20 to 30 years. Juniper cover decreased or remained relatively static for several years after the mid 1950s on untreated sites where the initial cover was >30% (see Irion and Coke Counties, Fig. 2). In contrast, juniper cover steadily increased, usually at increasing rates, on untreated rangeland where the initial canopy cover was <14% (see Crockett, Nolan, and Reagan Counties, Fig. 2). These differences suggest that, following the drought of the 1950s, intraspecific competition may have suppressed juniper growth and seedling recruitment rates on rangeland with heavy juniper cover, whereas adequate resources were available for growth and seedling recruitment on rangeland with light juniper cover.

The rate of juniper canopy cover change on untreated rangeland increased over time from the mid 1960s through 1996 at most sites (Fig. 2). Terminal rates of canopy cover change on untreated rangeland varied from 0.45 percentage units year^{-1} in Irion County, where cover was approaching 38%, to 1.08 percentage units year^{-1} in Crockett County, where cover was approaching only 26% (Fig. 2). The Crockett County untreated site supported only 11% juniper cover in 1985, which was much less than was present on the other untreated sites. This suggests that the environment of the Crockett County site from 1985–1996 was capable of supporting more juniper cover, whereas juniper populations on other undisturbed sites may have been more mature and perhaps approaching equilibrium with their environments.

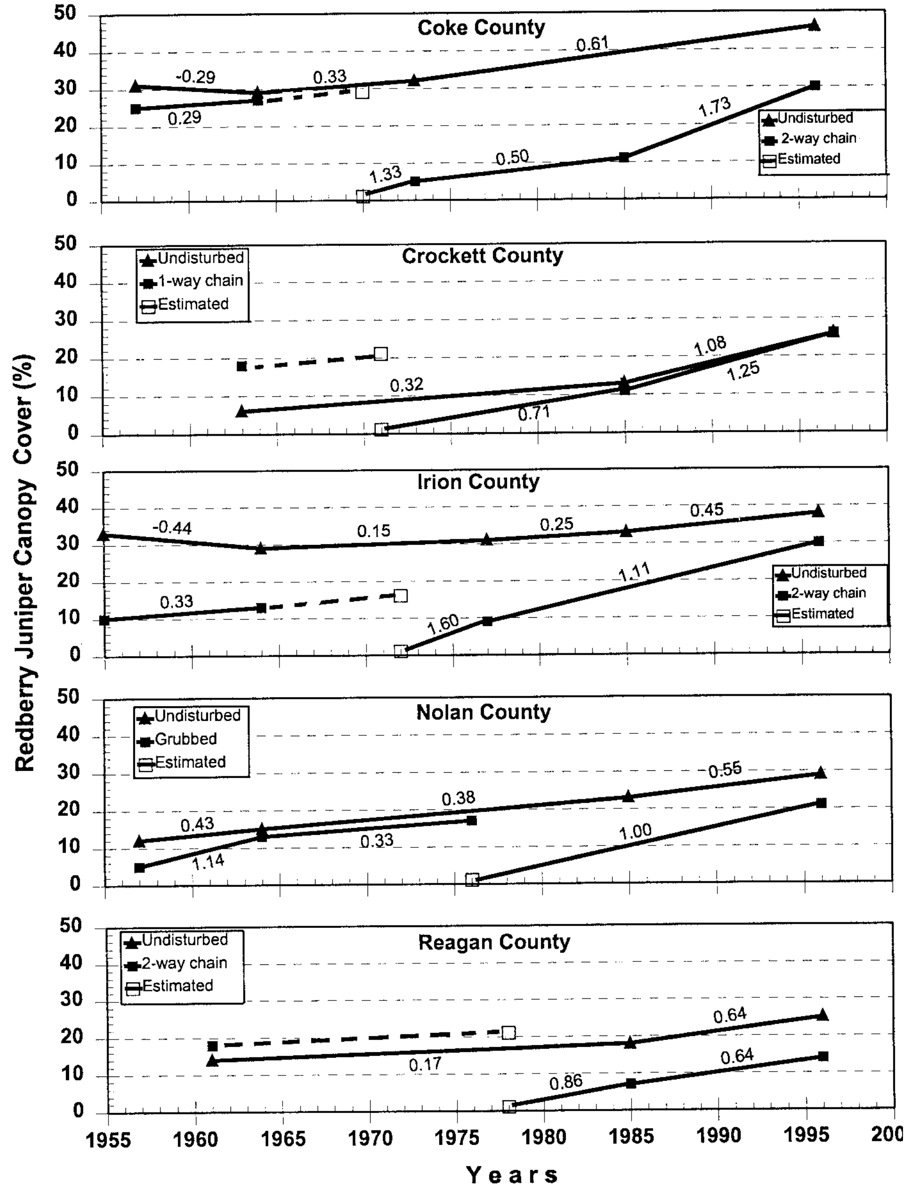

Fig. 2. Redberry juniper canopy cover (%) from 1955 to 1997 on undisturbed rangeland and adjacent sites subjected to chaining or grubbing in Coke, Crockett, Irion, Nolan, and Reagan Counties, Tex. estimated from aerial photographs. Numbers between data points are the rates of canopy cover change (percentage units year^{-1}). Standard errors of the means were too small (avg. 0.98, range 0.33 to 2.32) to show with vertical lines.

Regression analysis revealed that the long-term rate of change in juniper canopy cover over 34- to 41-year periods on untreated sites was 0.35 ± 0.06 percentage units year^{-1} ($P < 0.001$) (range 0.12 to 0.59). There were significant differences among sites for canopy cover, but regression coefficients were not different among the sites ($P > 0.10$). The untreated site in Irion County, which supported the greatest initial juniper cover (33%) (Fig. 2), had the lowest long-term rate of change (0.12). The site with the greatest long-term rate of change (0.59) was in Crockett County where average annual rainfall was similar to that for Irion County (Fig. 3), but where the initial juniper canopy cover was lowest (6%) (Fig. 2). Regression analyses revealed no significant relationships between the long-term rate of juniper cover change and initial juniper cover,

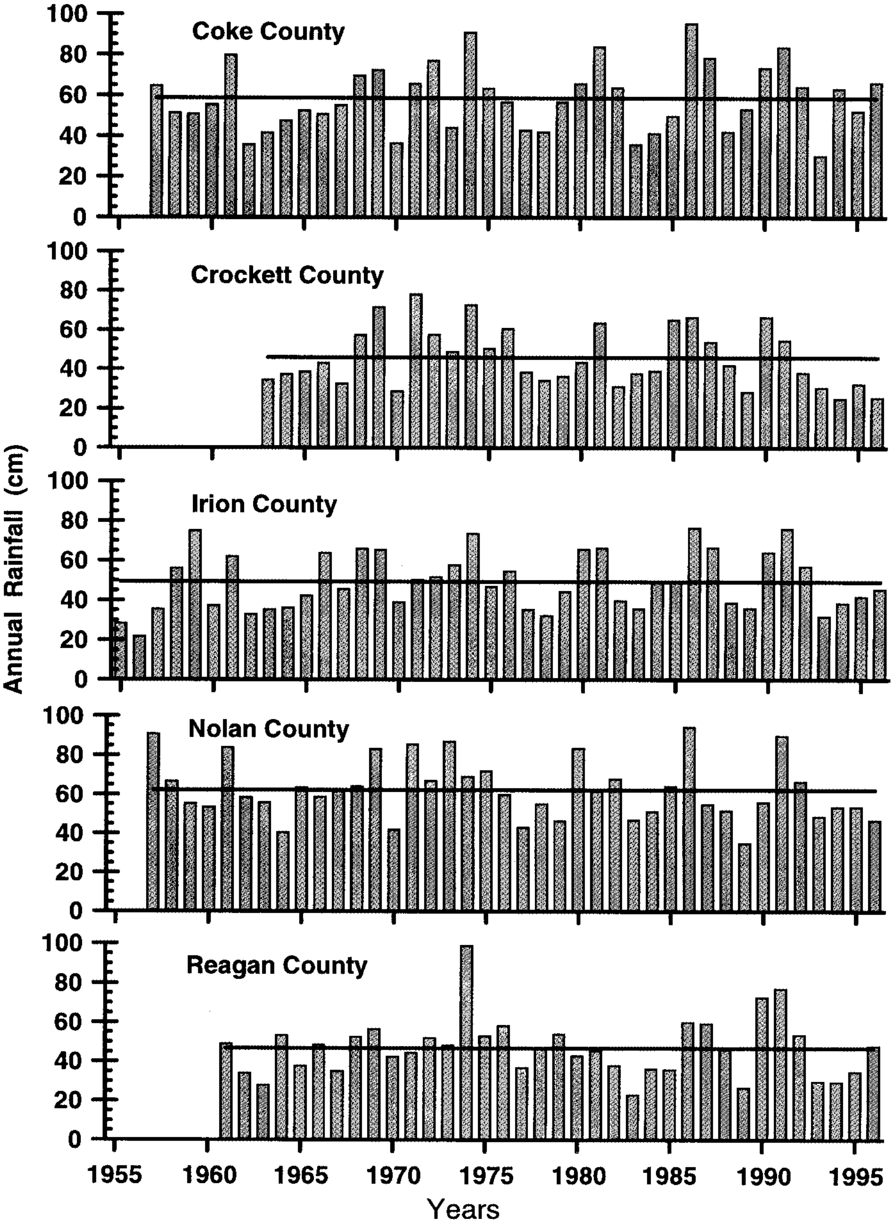

Fig. 3. Annual rainfall for the study periods (years covered by aerial photographs) for redberry juniper study sites in Coke, Crockett, Irion, Nolan, and Reagan Counties, Tex. Horizontal lines represent average annual rainfall for the study period.

average annual rainfall, or median annual rainfall on the 5 untreated sites ($P > 0.10$). We speculate that interactions among many factors, including initial juniper cover, initial abundance of juvenile juniper plants, seedling recruitment rates, climatic variables that impact juniper growth and recruitment, and competition from the herbaceous understory would collectively account for the variation among sites in the long-term rate of juniper cover change. Redberry juniper is most likely to establish during cool, wet periods (Smith et al. 1975). McPherson and Wright (1990b) found that over half the redberry juniper seedlings at study sites in the High Plains and Rolling Plains of Texas established during the second year of 2-year periods of above-average precipitation. Successive years with above-average precipitation at all our study sites (Fig. 3) may account for the continual growth of these juniper woodlands.

Mechanically Treated Rangeland

Regression analysis indicated that the rate of increase in juniper canopy cover over 18- to 26-year periods following chaining or grubbing was 1.01 ± 0.07 percentage units year^{-1} ($P < 0.0001$) (range 0.72 in Reagan County to1.21 in Irion County). Site was not a significant source of variation ($P > 0.4$) for canopy cover on the treated sites and regression coefficients were not different among sites ($P > 0.10$). The rate of increase in juniper cover on treated sites was greater than the rate of 0.50 ± 0.13 percentage units year^{-1} that occurred during the same time interval (1970-78 to 1996-97) on untreated sites ($P = 0.001$).

Juniper cover returned to estimated pretreatment levels (avg. 21%) in an average of 20 years (range 11 to 25 years) following chaining or grubbing at 4 of the treated sites (Fig. 2). Juniper cover had not returned to the estimated pre-treatment level by 1996 at the treated site in Reagan County. Regression analyses revealed that there were no relationships between the rate of juniper canopy cover increase following mechanical control and average or median annual precipitation or pre-treatment juniper cover at the sites studied ($P > 0.10$).

The rapid development of juniper cover following mechanical control can be attributed to 3 factors. Redberry juniper seedlings and saplings are often abundant in the understory of mature junipers in the Edwards Plateau (Ueckert and Whisenant 1982, Dye et al. 1995) and these small plants are not effectively controlled by chaining or grubbing. Chaining and grubbing reduce the competitive effects that mature junipers have on growth of these juvenile plants and they grow rapidly. On some sites, chaining simply removes the aboveground portion of large redberry junipers and these resprout from the basal caudex. Competition from associated vegetation has little impact on the growth rate of these plants. The growth rate of a resprouting juniper can approach 1,400 cm^3 year^{-1} (McPherson and Wright 1989). Also, the soil disturbance and juniper debris created by chaining and grubbing provides seedbeds and safe sites for juniper seed germination and seedling establishment.

Relationship of Juniper Cover, Herbage Production, and Time

The Johnson et al. (1999) natural log model predicted the declining trend in annual herbage production over time shown in Fig. 4 for untreated rangeland, utilizing 0.35 percentage units year^{-1} as the rate of increase in redberry juniper cover as cover thickens from 6 to 46%. The mathematical model which fit this trend

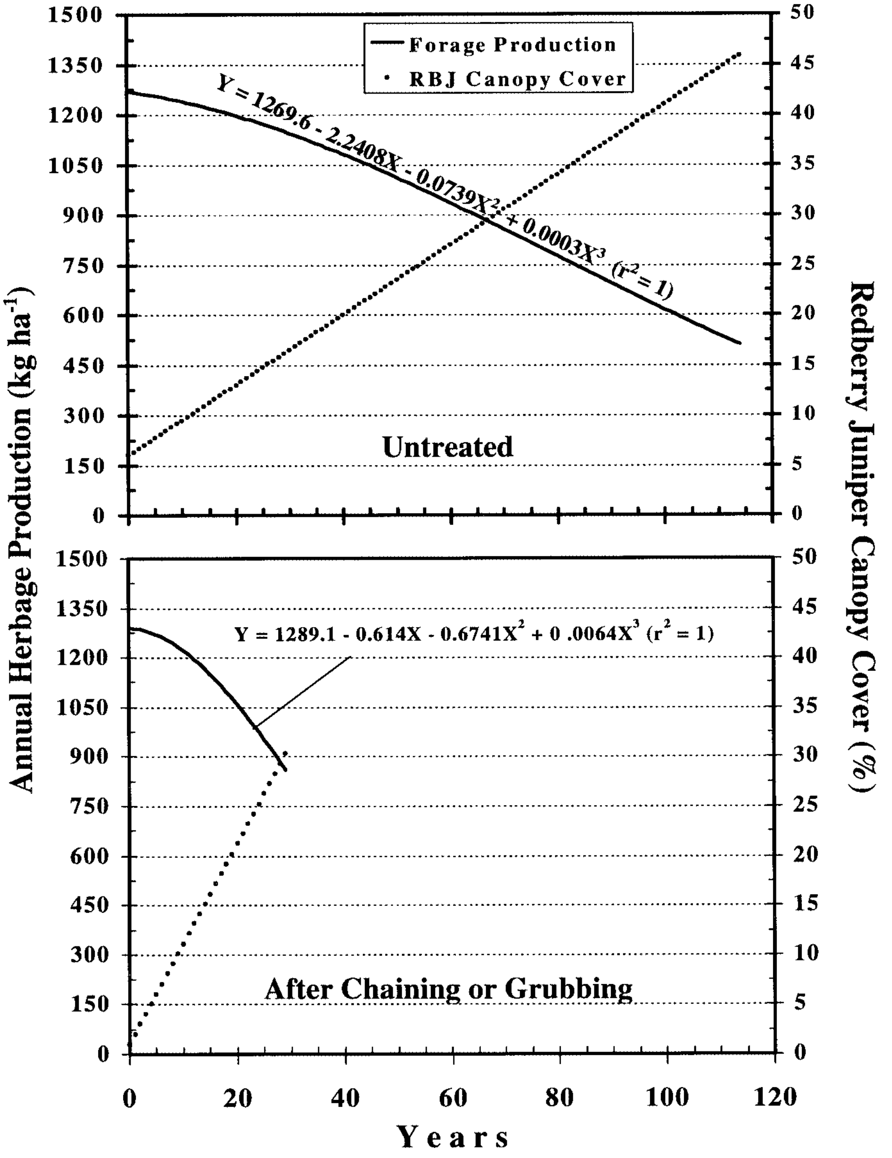

Fig. 4. Predicted trends in annual herbage production (kg ha^{-1}, Y) as a function of time (years, X) for untreated and treated redberry juniper study sites. The curves were developed by integrating our estimates of annual redberry juniper canopy cover (%) into a natural log model of the relationship between annual herbage production and redberry juniper canopy cover (Johnson et al. 1999). The r^2 value is 1.00 because the level of forage production estimated for a given level of juniper cover by the natural log equation is equal to the level of forage production estimated by the cubic equation using time (years) required for juniper cover to reach this level as the independent variable. Annual juniper canopy cover (dotted line) is included in each graph for reference only.

line was $Y = 1269.6 - 2.2408X - 0.0739X^2 + 0.0003X^3$, where Y = annual herbage production (kg ha^{-1}) and X = time (years) ($r^2 = 1.00$). The r^2 value is 1.00 because Johnson's natural log equation and our cubic equation are equivalent forms of the same relationship, i.e., the level of forage production estimated for a given level of juniper cover by the natural log equation is equal to the level of forage production estimated by the cubic equation using time (years) required for juniper cover to reach this level as the independent variable. The model indicates that annual herbage production declines at an increasing rate for about 80 years, or until juniper cover reaches 34%, and then declines at a decreasing rate. The annual increments in herbage production decline were relatively low (2.4 to 5.0 kg ha^{-1}) during years 0 through 22 as juniper cover increased from 6 to 14% and greatest (>8 kg ha^{-1}) during years 68 through 92 as juniper cover increased from 30 to 38%. The model predicted that annual forage production would decrease by 60% (760 kg ha^{-1}) as juniper cover increased from 6 to 46% over a period of 115 years (Fig. 4).

Using 1.01 percentage units year^{-1} as the rate of increase in juniper cover following mechanical control, the Johnson et al. (1999) natural log model predicted the decline in annual herbage production shown in Fig. 4 as juniper cover increased from 1 to 30%. The mathematical model $Y = 1289.1 – 0.614X – 0.6741X^2 + 0.0064X^3$, where Y = annual herbage production (kg ha^{-1}) and X = time (years) fit these data ($r^2 = 1.00$). This model predicted that the decline in annual herbage production would increase at a constantly increasing rate from < 2 kg ha^{-1} yr^{-1} in year 1 up to 23 kg ha^{-1} yr^{-1} in year 29. Annual forage production would decline by 33% (429 kg ha^{-1}) over a 29-year period post-treatment as juniper cover increased from 1 to 30% (Fig. 4).

Effect of Juniper Control on Livestock Carrying Capacity

Economists must have some measure of production response to treatment over a realistic time frame to estimate the economic feasibility of alternative brush management practices (Conner 1985). The estimated impacts of controlling redberry juniper when infestations are at 20 and 30% canopy cover upon livestock carrying capacity are shown in Fig. 5. The treatment life of mechanical juniper control at 20% canopy cover was predicted at 19 years for carrying capacity to return to the pretreated production level (TL_1) and 29 years for carrying capacity of treated land to return to levels without treatment (TL_2) (Fig. 5). The corresponding values for additional livestock carrying capacity (ACC_1 and ACC_2) due to treatment at 20% juniper cover were 38 and 71 A.U.Y. 259^{-1} ha for the 19- and 29-year periods, respectively. The treatment life was predicted at 29 and 44 years for TL_1 and TL_2, respectively, when juniper was controlled at 30% canopy cover (Fig. 5). Additional livestock carrying capacity due to treatment at 30% cover was 116 and 197 A.U.Y. 259^{-1} ha for the 29- and 44-year periods, respectively. Researchers have relied upon hypothetical response curves and the assumption that the level of production without treatment remains constant throughout the planning profile in some economic analyses of woody plant management practices (Conner 1985). Our data provide useful information which

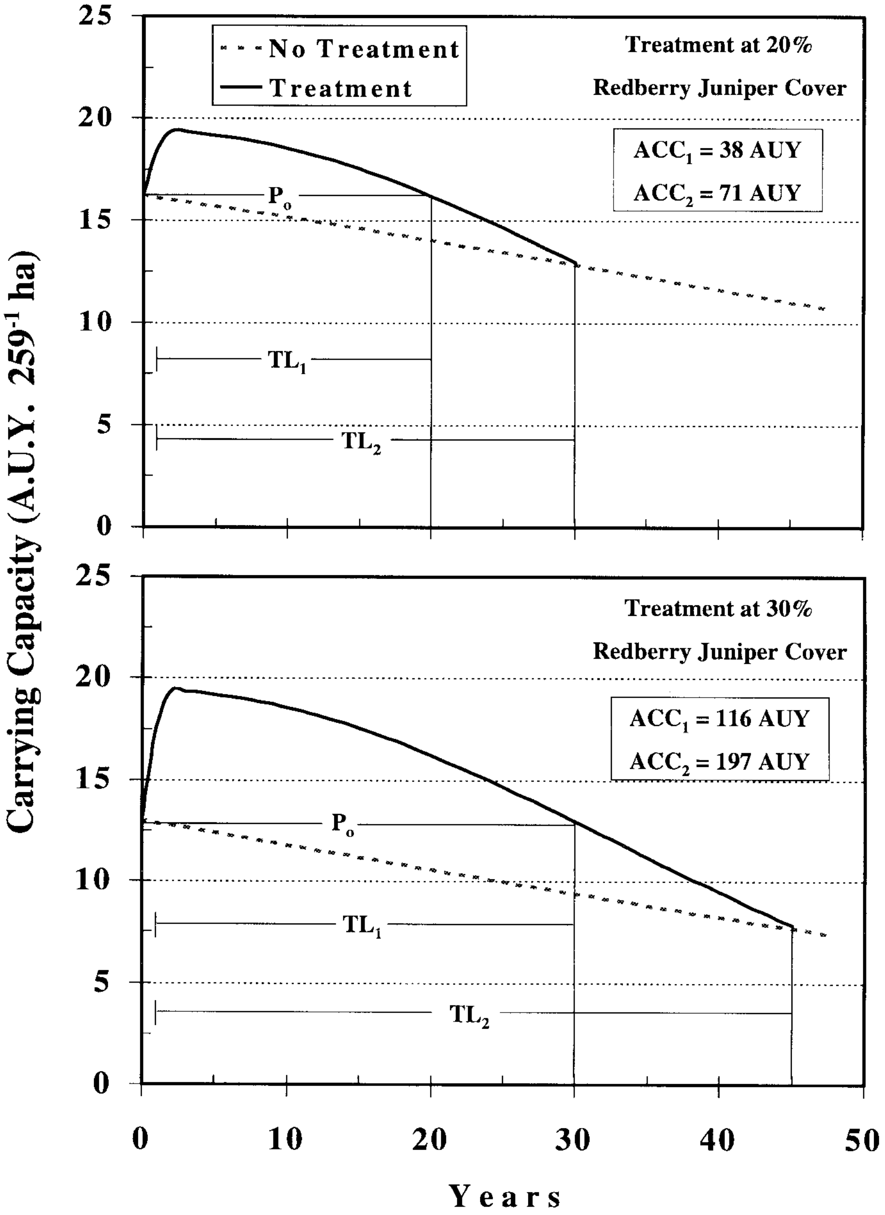

Fig. 5. Predicted livestock carrying capacity [A.U.Y. 259^{-1} ha, Y] as a function of time (years, X) for untreated rangeland and rangeland treated for juniper control at 20 or 30% juniper canopy cover. P_0 is the pretreatment production level. Treatment was applied in year 1. TL_1 is the time (years) for production of treated rangeland to return to P_0. TL_2 is the time (years) for production of treated rangeland to return to the level without treatment. ACC_1 and ACC_2 values are the additional carrying capacities (A.U.Y.) due to treatment for TL_1 and TL_2 in each scenario.

economists can use to project annual production levels and realistic estimates of treatment life for redberry juniper control practices. The major differences between ACC_1 and ACC_2 values shown above definitely do not support use of the assumption that the level of production without treatment remains constant throughout the planning profile. ACC_1 values were >40% lower than ACC_2 values.

Management Implications

The threshold from grasslands, in which graminoid-driven successional processes predominate, to redberry juniper-dominated woodlands is crossed when sufficient numbers of juniper become established and reach reproductive maturity. At this point, juniper-driven successional processes become predominant, including: (1) a general reduction in diversity, density, basal area, and productivity of herbaceous plants; (2) an influx of secondary woody and succulent species; (3) further reduction in fire frequency and intensity; and (4) a high incidence and rate of additional juniper seedling recruitment (Dye et al. 1995). This study documents the rates at which redberry juniper woodlands develop and recover following chaining or grubbing and concomitant rates in decline of herbage production and carrying capacity. This study also substantiates the conclusion of Dye et al. (1995) that conversion of juniper woodlands back to grasslands will not only require initial reclamation treatments, but also maintenance control practices and proper grazing management. Redberry juniper canopy cover will increase at the rate of 1.01 percentage units $year^{-1}$ following mechanical control, thus the effective treatment life of a practice that reduces juniper cover by 20% will be about 20 years.

Our data show that annual herbage production on untreated juniper woodlands declines slowly as redberry juniper cover reaches about 14% but rapidly as juniper cover continues to increase above 20%. We suggest that initial or maintenance control practices should be installed before redberry juniper cover exceeds 20%, i.e. before annual herbage production begins declining at peak rates.

Knowledge of the rate of change in woody plant canopy cover is essential for estimating the expected treatment life of control practices and the decline in herbage production without treatment. This study provides quantitative information that should be helpful for studying the profitability of alternative juniper management practices. In a recent study of the economic feasibility of redberry juniper control using two-way chaining as the initial treatment and periodic prescribed burning as maintenance treatments, Johnson et al. (1999) utilized empirical rates of juniper cover change of 1.6, 2.5, and 5 percentage units $year^{-1}$. Their study showed that net present value of juniper control treatments increased from $67 to $130 ha^{-1} and that the optimal burning cycle decreased from 9 to 5 years as the rate of juniper cover change increased from 1.6 to 5 percentage units $year^{-1}$. The lower rates of increase in juniper cover that we report in this study (0.35 and 1.01 percentage units $year^{-1}$ for untreated and treated rangeland, respectively) suggest that the net present value of controlling juniper with chaining and periodic burning would be substantially less than $67 ha^{-1}, and that the optimum burning interval would be longer than 9 years. The major differences in estimated productivity of treated and untreated rangeland reported in this study clearly indicate that it should not be assumed in economic studies that production of untreated rangeland would remain constant over the planning period. Ranchers and rangeland resource managers should recognize that excessive grazing pressure gives juniper, which is relatively unpalatable, a competitive advantage over palatable forage species. Failure to reduce stocking rates as juniper cover increases will likely accelerate the rate of increase in juniper cover and the rate of decrease in herbage production and livestock carrying capacity.

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Quantifying suitable habitat of the threatened western prairie fringed orchid

PAIGE M. WOLKEN, CAROLYN HULL SIEG, AND STEPHEN E. WILLIAMS

Authors are botanist, U.S. Fish and Wildlife Service, Utah Field Office, 145 East 1300 South, Suite 404, Salt Lake City, UT 84115; research plant ecologist, USDA Forest Service Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, Ariz. 86001; and dean of the Graduate School, University of Wyoming, Laramie, Wyoming 82071. At the time of the research, Wolken was graduate student, Department of Plant, Soil, and Insect Sciences, University of Wyoming, Laramie, Wyo., 82071; Sieg was research wildlife biologist, USDA Forest Service Rocky Mountain Research Station, Rapid City, S.D.; and Williams was professor and Department Head, Department of Plant, Soil, and Insect Sciences, University of Wyoming, Laramie, Wyo. Carolyn's e-mail address is csieg@theriver.com

Abstract

Land managers need accurate and quick techniques to identify suitable habitat of species of interest. For species protected by federal or state laws, identification of suitable habitat is critical for developing a conservation strategy that includes reestablishing populations and altering management to address this need. In this research, we quantified vegetative and edaphic habitat of the western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles), a federally listed threatened plant. Lowlands (swales) that supported orchids in our southeastern North Dakota study area were characterized as having a higher soil moisture content within the top 10 cm, when compared to swales devoid of orchids. The vegetative composition of orchid-supporting swales reflected this higher moisture content. These data were then used in developing a logistic regression model to differentiate suitable habitat. The model correctly classified 84% of 38 swales as either orchid-supporting or non-orchid-supporting using 4 variables: percent canopy cover of Baltic rush (*Juncus balticus* Willd.) and hedge-nettle *(Stachys palustris* L.*)*, soluble soil magnesium and August surface soil moisture. Land managers can use this model to rapidly assess the suitability of a site in this ecoregion for the orchid. By collecting data on the cover of just Baltic rush, which would take about 45 minutes, and entering it in the equation, a land manager could correctly classify 66% of the orchid swales as either suitable or unsuitable as orchid habitat. This approach, because it incorporates quantitative data and allows managers to rapidly and accurately identify suitable habitats, shows promise for other plant species.

Key Words: *Platanthera praeclara*; wetland; tallgrass prairie; threatened plant; edaphic factors; logistic regression; soil moisture; North Dakota.

Resumen

Los administradores de tierras necesitan tecnicas precisas y rapidas para identificar habitat adecuado de especies de interes. Para especies protegidas por leyes federales o estatales, la identificacion de habitat adecuado es critico para desarrollar una estrategia de conservacion que incluya el reestablecimiento de poblaciones y adecuar el manejo de acuerdo a estas necesidades. En esta investigacion, cuantificamos el habitat vegetativo y edafico de la orquidia del borde de la pradera oriental (*Platanthera praeclara* Sheviak and Bowle), una planta enlistado federalmente como amenazada. Tierras inundables (cienegas) que soportan estas orquideas en nuestra area de estudio en el sureste de North Dakota fueron caracterizadas como de mas alto contenido de humedad en los primeros 10 cm del suelo, cuando se comparan con las cienegas sin orquideas. La composicion vegetal de las cienegas que soportan orquideas reflejan este mas alto contenido de humedad. Estos datos fueron usados para desarollar un modelo de regresion logistica para diferenciar habitat adecuado. El modelo clasifico correctamente el 84% de 38 cienegas como adecuados o inadecuados para las orquideas usando cuatro variables: porcentajes de coberturas de junco Baltico (*Juncus balticus* Wiilld.) y ortiga (*Stachys palustris* L.), magnesio soluble en el suelo y humedad superficial del suelo en Agosto. Administradores de tierras pueden usar este modelo para evaluar rapidamente la aptitud de un sitio para las orquideas en esta ecoregion. Colectando datos de cobertura solamente de junco Baltico, que tomaria cerca de 45 minutos, y metiendolos en la ecuacion, un administrador podria clasificar correctamente un 66% de cienegas como habitat adecuadas o inadecuadas para orquideas. Este enfoque, porque incorpora datos cuantitativos y permite a los administradores identificar habitat adecuado con rapidez y precision, parece prometedor para otras especies de plantas.

Land managers need quantitative techniques to rapidly assess the suitability of habitats for rare plant species. This information may be used to delineate special management areas or to identify potential reintroduction sites. Establishment of new populations is imperative for the recovery and eventual delisting of threatened and endangered plant species (Schemske et al. 1994). Success of establishment efforts is greatest when individuals are replanted in the same microhabitat from which they were collected (Holsinger and Gottlieb 1991).

The western prairie fringed orchid *(Platanthera praeclara* Sheviak and Bowles) was listed as a threatened plant in 1989

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(U.S. Fish and Wildlife Service 1989). Its rarity is attributed to the conversion of most of the tallgrass prairie to croplands or other development (Samson and Knopf 1994). Currently, only 3 metapopulations of the orchid are known: 2 in the United States and 1 in Manitoba (U.S. Fish and Wildlife Service 1996). The North Dakota metapopulation is in the southeastern corner of the state, almost entirely on the Sheyenne National Grassland, in sedge meadows associated with lowland depressions (swales) (Sheviak and Bowles 1986, Bjugstad and Fortune 1989, Sieg and Bjugstad 1994). Although many subirrigated swales on the Sheyenne National Grassland support populations of the western prairie fringed orchid, there are also swales that do not support orchids. The objectives of this study were to: 1) isolate vegetative and edaphic factors associated with the patchy distribution of the western prairie fringed orchid, and 2) develop a technique (model) that can be used to differentiate between suitable and unsuitable habitat.

Materials and Methods

A paired design was chosen to compare environmental factors between swales that supported orchids and swales that did not. Using baseline data collected over the previous 7 years, 19 swales with a minimum of 10 orchids each were selected from the core of the Sheyenne National Grassland metapopulation. In addition, for each swale supporting orchids, we selected a nearby swale without orchids, for a total of 19 non-orchid swales. Criteria used in selecting non-orchid swales included close proximity to an orchid swale and similar management, exposure and topography. Potential non-orchid sites were searched carefully for orchids—including the smaller vegetative plants—to ensure that the site was devoid of orchids. We attempted to cover the range of swale environments exposed to a seed source and therefore potentially capable of supporting the orchid. We established an oblong or circular plot in each of the 38 swales that, depending on the size and shape of the swale and distribution of the orchid population, ranged in size from 250 to 500 m^2. The plots were dispersed among 6 study sites on the Sheyenne National Grassland. Two thirds of the plots were grazed by cattle either season long or were in a three-pasture rotation system. The remainder of the plots were in exclosures or along the railroad right-of-way.

In July 1992, plant composition in orchid and non-orchid swales was characterized by estimating percent plant canopy cover in a minimum of 20 and up to fifty, 20 x 50 cm quadrats. Cover was estimated to fall in 1 of 6 cover classes (1 = 0-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96–100%) (Daubenmire 1959). Quadrats were systematically placed at 1-m intervals along permanent transects (20 to 50 m in length). Variables estimated included: total plant canopy cover, total graminoid cover, total shrub cover, total forb cover, litter, bare ground, and cover by species. We used Great Plains Flora Association (1986) for taxonomic determination and nomenclature. During the height of the flowering season (late June through early July) in 1992 and 1993, orchids were permanently marked with numbered marker pins and mapped using a coordinate system.

Soil moisture was estimated in July and August of 1992 and June of 1993. A probe (48 cm long x 2 cm diameter tube) was used to collect 4 soil samples per swale. Each sample was stratified into 4 depths: 0–2 cm, 2–10 cm, 10–20 cm, and 20–30 cm. Samples were collected 15 cm from 4 separate orchid plants in orchid swales and randomly in non-orchid swales. Soil moisture was determined gravimetrically (dried at 105° C for 48 hours). In 1993, soils were completely saturated due to flooding. Therefore, depth of standing water was measured at 4 random points in each swale in July and August of 1993.

Additional soil samples were collected in August 1992 for chemical analyses. A total of 4 samples (10 cm deep by 4 cm diameter) were collected 15 to 20 cm from 4 separate orchid plants in each orchid swale and randomly in each non-orchid swale. Approximately 700 g of soil was taken per sample, stored in plastic bags and frozen for subsequent total nitrogen testing. Chemical analyses, conducted at the University of Wyoming Soil Testing Laboratory,Laramie, Wyo. included pH, electrical conductivity (EC), soluble cations: potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), and soluble sulfur (S), percent calcium carbonate ($CaCO_3$) (Richards 1954), percent total nitrogen (N) (Jones 1971), nitrate (NO_3) (Sims and Jackson 1971), available phosphate phosphorous (PO_4) (Olsen and Sommers 1982), percent organic matter (OM) (Greweling and Peech 1960), percent water at saturation, and texture (mechanical) (Day 1965).

Statistical Analysis

We designed the study to use paired t-tests to test for differences in vegetative composition, soil moisture, water depth, and soil chemistry between orchid and non-orchid swales. Assumptions of normality were tested with Lilliefors Test; the variances were tested using the Levene Test (Norusis 1990). The data for 42 of 51 variables were not normally distributed ($P < 0.05$). Elimination of extreme outliers and data transformation did not correct non-normality nor heterogeneous variances. Therefore, we used the Wilcoxon signed-rank test to compare variables between orchid and non-orchid swales. Significance of Wilcoxon signed-rank tests was estimated using Monte Carlo estimates of exact P-values based on 10,000 repeated samples, thus avoiding the assumptions attached to using the asymptotic P-values (Mehta and Patel 1995). We set $\alpha = 0.05$ for all tests.

We utilized logistic regression to identify variables that are most useful or “most likely” to distinguish between two classes (Press and Wilson 1978, Hosmer and Lemeshow 1989). Logistic regression provides an equation to predict the probability that a swale will support orchids and a multivariate comparison between orchid and non-orchid swales, plus it identifies those variables most associated with the presence and absence of orchids. The selection and contribution of each variable depends on the other variables in the model, so highly correlated variables may greatly influence the final model. We used a correlation matrix to identify these variables. Only 1 of a pair of highly correlated ($r > 0.85$) variables was used in the model; the variable with the least biological importance was eliminated. We applied forward stepwise logistic regression with the likelihood-ratio test. Misclassification rates for logistic regression models were estimated using “leave-one-out” cross-validation, which makes more efficient use of small data sets that are common in studies of rare species. This cross-validation method involves refitting the model by leaving 1 observation out, and then computing the predicted value for the *i*th observation; this is done for each observation at each step and then the average cross-validation sum of squares is computed (Efron and Tibshirani 1993). We summarized the average misclassification rate for orchid and non-orchid sites at each step. We used the SPSS/PC+ statistical package (Norusis 1990) to perform all analyses.

Table 1. Average (± SD) percent canopy cover of major plant species in orchid and non-orchid swales on the Sheyenne National Grassland, 1992.

Category Species	Swale Type Orchid	 Non-orchid
	- - - - - - - - - - - (%)	- - - - - - - - - - -
Total Cover	83.7 ± 8.7	82.4 ± 5.3
Total Litter	93.9 ± 4.2	89.2 ± 12.5
Bare ground	1.5 ± 2.1	5.5 ± 8.2
Total Forb Cover	41.4 ± 15.7	33.9 ± 15.8
western ragweed (*Ambrosia psilostachya* DC.)	4.7 ± 6.4	6.1 ± 5.9
meadow anemone *(Anemone canadensis* L.*)*	6.7 ± 10.7	2.8 ± 3.5
panicled aster *(Aster simplex* Willd.*)*	7.6 ± 8.7	4.0 ± 3.8
smooth scouring rush *(Equisetum laevigatum* A. Br.*)*	1.4 ± 2.4	1.2 ± 1.5
leafy spurge (*Euphorbia esula* L.*)*	5.2 ± 10.0	2.9 ± 4.6
euthamia (*Euthamia graminifolia* (L.) Nutt.*)*	1.8 ± 3.5	2.2 ± 3.1
wild strawberry *(Fragaria virginiana* Duchn.*)*	4.3 ± 7.0	4.3 ± 9.5
wild licorice (*Glycyrrhiza lepidota* Pursh)	0.7 ± 1.0*	4.4 ± 6.5
water smartweed *(Polygonum amphibium* L.*)*	1.3 ± 2.6	0.8 ± 1.6
Canada goldenrod *(Solidago canadensis* L.*)*	2.8 ± 2.9	3.2 ± 4.4
hedge-nettle *(Stachys palustris* L.*)*	1.0 ± 1.8**	0.0 ± 0.0
Total Graminoid Cover	65.8 ± 20.2	66.9 ± 14.6
big bluestem (*Andropogon gerardii* Vitman)	0.1 ± 0.3	3.7 ± 9.4
little bluestem *(Schizachyrium scorparium* Michx.*)* Nash	0.0 ± 0.0	1.9 ± 8.5
northern reedgrass *(Calamagrostis stricta* (Timm.) Koel.*)*	14.7 ± 18.7	6.9 ± 8.6
Wilcox dicanthelium *(Dichanthelium wilcoxianum* (Vasey) Freckmann*)*	3.3 ± 8.6	1.5 ± 2.3
Baltic rush *(Juncus balticus* Willd.*)*	5.4 ± 5.1**	1.7 ± 1.9
switchgrass *(Panicum virgatum* L.*)*	6.2 ± 6.6	4.9 ± 6.3
Kentucky bluegrass (*Poa pratensis* L.)	18.2 ± 21.5	22.3 ± 16.1
Indian grass *(Sorghastrum nutans* (L.) Nash*)*	0.8 ± 1.9	5.7 ± 11.9
reed canary grass *(Spartina pectinata* Link*)*	4.3 ± 7.4	3.4 ± 5.5
sedges *(Carex* L. spp.[1]*)*	11.1 ± 9.2	15.3 ± 11.5
Total Shrub Cover	14.2 ± 14.6	11.3 ± 16.9
lead plant *(Amorpha canescens* Pursh*)*	0.1 ± 0.1	1.1 ± 2.4
white sage *(Artemisia ludoviciana* Nutt.*)*	0.0 ± 0.1	1.1 ± 4.4
willows (*Salix* L. spp.[2])	11.9 ± 12.3	7.2 ± 11.3

[1] Includes *Carex lanuginosa* Michx., *C. brevior* (Dew.) Mack. ex Lunell, and *C. granularis* Muhl. ex Willd.
[2] Includes *Salix exigua* Nutt. and *S. bebbiana* Sarg.
** Orchid and non-orchid swales significantly different (P ≤ 0.01)
* Orchid and non-orchid swales significantly different (P ≤ 0.05)

Results

Associated Vegetation

Orchid and non-orchid swales did not differ significantly (P > 0.05) in total plant canopy cover, litter cover, forbs, total graminoids, shrubs or bare ground (Table 1). Cover of wild licorice *(Glycyrrhiza lepidota*) (plant authorities are found in Table 1) was lower (P = 0.03) in orchid swales and cover of hedge-nettle *(Stachys palustris)* was higher (P = 0.002) in orchid swales. Leafy spurge *(Euphorbia esula)* was present in both swale types. Cover of Baltic rush *(Juncus balticus)* was higher (P = 0.01) on orchid swales compared to non-orchid swales. Kentucky bluegrass *(Poa pratensis)* and willows, including *Salix exigua and S. bebbiana*, were common on both swale types with similar (P > 0.05) cover values.

Soil Moisture

Surface soil moisture was consistently higher in orchid swales than in non-orchid swales (Table 2). July 1992 (P = 0.004), August 1992 (P = 0.002), and June 1993 (P = 0.05) soil moisture in the top 2 cm of soil was higher in orchid swales (24–52%), compared to non-orchid swales (16–45%). In addition, soil moisture at the 2- to 10-cm depth was higher in orchid swales than in non-orchid swales in August 1992. Soil moisture at greater depths (10–30 cm) did not differ between orchid and non-orchid swales.

Standing Water

Standing water depths in 1993 varied greatly within and among swales. In July, the water depth in orchid swales averaged 28.3 cm (± 18.9 SD), compared to an average of 13.3 cm (± 12.7 SD) (P = 0.001) in non-orchid swales. The maximum depth of standing water in orchid and non-orchid swales was 80 cm and 43.6 cm, respectively. The depth of standing water in August 1993 declined in most swales, but remained significantly higher (P = 0.007) in orchid swales (13.5 cm ± 12.2 SD) compared to non-orchid swales (4.3 cm ± 6.7 SD). Maximum water depths in August were 45.0 and 31.8 cm, respectively, for orchid and non-orchid swales; but some swales of both types had no standing water in 1993.

Soil Chemistry and Texture

With the exception of soluble magnesium, soil chemistry was similar in the 2 swale types (Table 3). Within the upper 10 cm of soil, soluble magnesium was significantly higher (P = 0.002) in non-orchid swales than in orchid swales. In general, the upper 10 cm of soil in all swales could be described as a neutral to slightly alkaline, fertile sandy loam. The range of soil textures included sand, loamy sand, sandy clay loam, and loam. The percentage sand (70%, ± 11.7 SD - orchid; 70% ± 14 SD - non-orchid), silt (16% ± 7.1 SD - orchid; 15% ± 7 SD - non-orchid), and clay (14%, ± 5.6 SD - orchid; 15% ± 7.4 SD - non-orchid) did not differ (P > 0.05) between orchid and non-orchid swales.

Table 2. Average (± SD) gravimetric soil moisture for orchid and non-orchid swales in July and August 1992 and June 1993, by depth on the Sheyenne National Grassland.

Depth	Swale Type	July 1992	August 1992	June 1993
(cm)		- - - - - - - - - - -	- - - - - - (%) - - - - - -	- - - - - - - - - - -
0-2	orchid	26.3 ± 7.7**	23.9 ± 8.9**	51.9 ± 17.0
	non-orchid	21.2 ± 6.0	16.3 ± 13.0	44.8 ± 15.5
2-10	orchid	30.3 ± 11.5	30.6 ± 13.7*	41.3 ± 15.0
	non-orchid	26.9 ± 13.2	24.9 ± 14.3	34.9 ± 15.7
10-20	orchid	19.9 ± 5.4	20.0 ± 6.9	25.0 ± 6.0
	non-orchid	20.4 ± 9.9	18.3 ± 9.6	24.3 ± 8.5
20-30	orchid	14.5 ± 3.9	14.9 ± 11.3	20.4 ± 4.5
	non-orchid	13.8 ± 5.1	12.7 ± 4.9	18.3 ± 5.5

**Orchid and non-orchid swales different (P < 0.01)
*Orchid and non-orchid swales different (P < 0.05)

Table 3. Average (± SD) nitrogen (N), organic matter (OM), calcium carbonate ($CaCO_3$), pH, electrical conductivity (EC), phosphate phosphorous (PO_4) P, nitrate (NO_3) N, potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), sulfur (S), and water at saturation for orchid and non-orchid swale soils on the Sheyenne National Grassland, 1992.

Analysis	Swale Type Orchid	 Non-orchid
N (%)	0.5 ± 0.4	0.5 ± 0.4
OM (%)	6.8 ± 5.5	5.1 ± 2.6
$CaCO_3$ (%)	9.3 ± 8.1	8.8 ± 8.4
pH	7.7 ± 0.2	7.6 ± 0.5
EC (ds/m)	0.7 ± 0.1	0.7 ± 0.2
PO_4 P (mg/kg)	8.7 ± 5.0	8.2 ± 3.1
NO_3 N (mg/kg)	13.2 ± 9.5	11.2 ± 7.7
K (meq/l)	0.3 ± 0.3	0.4 ± 0.3
Na (meq/l)	0.5 ± 0.2	0.4 ± 0.2
Mg (meq/l)	2.1 ± 0.8**	2.9 ± 1.3
Ca (meq/l)	4.9 ± 0.8	4.3 ± 1.5
S (mg/kg)	20.4 ± 12.0	18.5 ± 8.2
H_20 at saturation (%)	87.9 ± 35.2	78.5 ± 30.6

**Orchid and non-orchid swales different ($P < 0.01$).

Logistic Regression

The logistic regression analysis included 36 of the 51 independent variables (Table 4). These variables made sense biologically and were not highly correlated with each other. Percent cover of Baltic rush was the most useful variable in differentiating swales that support orchids from swales that did not (Table 5). With just Baltic rush in the model, the equation correctly classified 68% of orchid swales and 63% of non-orchid swales (Table 6). The addition of cover of hedge-nettle increased the percentage of swales correctly classified to an average of 71% for the 2 swale types. The addition of soluble magnesium enhanced the percentage of correctly classified swales to 79%. August soil moisture at the depth of 0–2 cm was the last variable to enter the equation. The final model correctly classified 84% of both the orchid and non-orchid swales:

Probability of an orchid swale =

$$1/ [1 + \exp (-1.10 + 0.60JUBA + 3.53STPA - 0.23Mg + 0.32ASM2)] \quad \textbf{(1)}$$

where JUBA = Baltic rush canopy cover, STPA = hedge-nettle canopy cover, Mg = soil magnesium, and ASM2 = August surface soil moisture.

Discussion

Managers need an understanding of habitat requirements of individual plants, and their relationship with other species and environmental parameters. Managers also need techniques that can be used to assess the quality of potential sites so they can alter management in areas likely to support threatened and endangered species or identify sites where reintroductions are more likely to be successful. This study provided a better understanding of the vegetation and soils of sites that supported the threatened western prairie fringed orchid, compared to sites devoid of this plant. We used these data to develop a logistic regression model that allows managers to quickly (and quantitatively) assess the likelihood that a given site will support orchids.

Table 4. Independent variables included[1] in the logistic regression analysis used to identify those most useful in distinguishing between orchid and non-orchid swales on the Sheyenne National Grassland.

Cover (%) of:	Other Variables
Total plant canopy	August soil moisture: 0-2 cm
Total forb	August soil moisture: 10-20 cm
Ambrosia psilostachya	June soil moisture: 0-2 cm
Aster simplex	June soil moisture: 20-30 cm
Euphorbia esula	Total N (%)
Euthamia graminifolia	OM (%)
Fragaria virginiana	$CaCO_3$ (%)
Juncus balticus	pH
Polygonum amphibium	EC (ds/m)
Solidago canadensis	PO_4 (available) (meq/l)
Stachys palustris	NO_3 (meq/l)
Litter	K (soluble cation) (meq/l)
Total graminoid	Na (soluble cation) (meq/l)
Total *Carex spp.*	Mg (soluble cation) (meq/l)
Calamogrostis stricta	Ca (soluble cation) (meq/l)
Dichanthelium wilcoxianum	S (soluble cation) (meq/l)
Panicum virgatum	
Poa pratensis	
Spartina pectinata	
Total *Salix* spp.	

[1] Variables excluded from the logistic regression analysis included: June soil moisture (10-20 cm), August soil moisture (2-10, 20-30 cm), Canopy cover (%) of: *Amorpha canescens, Anemone canadensis, Andropogon gerardii, Schizachyrium scoparium, Artemisia ludovicana, Equisetum laevigatum, Glycyrrhiza lepidota, Sorghastrum nutans,* total shrubs, and % water at saturation.

In many respects, the vegetative composition of both swales that supported and did not support orchids was similar, and included mixed grass and sedge meadow species. The vegetative differences between swales that supported orchids and those without orchids were a reflection of moisture conditions. Orchid-supporting swales had higher canopy cover of Baltic rush and hedge-nettle, yet lower cover of wild licorice. Baltic rush often grows in slightly alkaline sites, and along with hedge-nettle, is associated with high moisture habitats such as prairie sloughs, seepages and marshes (Great Plains Flora Association 1986).

We found that soil moisture was important in influencing the distribution of orchids, yet soil chemistry (with the exception of magnesium levels) was a poor indicator of orchid habitat. Swales that supported orchids were characterized by consistently higher surface (0–2 cm) soil moisture and deeper water in 1993 compared to those swales lacking orchids. Further, surface soil moisture was 1 of 4 variables in the final equation that best distinguished orchid swales from non-orchid swales. These data support Sieg and King's (1995) findings that orchid densities were associated with high surface (0-4 cm depth) soil moisture.

Subsurface moisture (2–10 cm) may also influence orchid habitat. In another phase of this study, 60% of the orchids Wolken (1995) examined had their rooting systems entirely within 10 cm of the surface. Soil moisture below 10 cm was less important in influencing orchid presence or absence. Similar soil moisture readings below 10 cm for both swale types indicate that soil moisture levels below the maximum rooting depth (16 cm) are not as critical as soil moisture levels within the lateral root system range (2–10 cm).

Unfortunately, this study also verified the presence of invasive species that threaten the quality of orchid habitat on the Sheyenne National Grassland. The

Table 5. Results of logistic regression analysis of variables characterizing orchid swales and non-orchid swales on the Sheyenne National Grassland, 1992–1993.

Step number	Variable[1] entered	Log likelihood	Model[2] Chi-square	Improvement[3] Chi-square
1	JUBA	-26.34	10.3**	10.3**
2	STPA	-21.21	18.7**	8.4**
3	Mg	-17.00	25.4**	6.7**
4	ASM2	-13.66	35.0**	9.6**

[1] JUBA = *Juncus balticus* canopy cover (%); STPA = *Stachys palustris* canopy cover (%); Mg = soil magnesium (mg/l); ASM2 = 1992 August soil moisture (%) at a depth of 0-2 cm.

[2] The model chi-square tests the null hypothesis that there is no difference between the constant and the model presented; a small P value indicates a significant change in the model.

[3] The improvement chi-square tests the null hypothesis that the addition of a variable does not change the model; a small P-value indicates improvement of the model with the addition of that variable .

** significant at $P < 0.01$

strong presence of Kentucky bluegrass in these swales was consistent with other recent studies (Sieg and King 1995, Sieg and Bjugstad 1994, Bjugstad-Porter 1993). Kentucky bluegrass tends to dominate and out-compete other plants (Reader et al. 1994), and orchid density in some years on the Sheyenne National Grassland was negatively correlated with Kentucky bluegrass cover (Sieg and King 1995). The invasion of leafy spurge, a perennial noxious weed, is a serious threat to orchid habitats on the Sheyenne National Grassland (Sieg and Bjugstad 1994).

Management of existing orchid habitat on the Sheyenne National Grassland should focus on sustaining the moist swales that support the orchid and its key vegetative associates. In the long run, sustaining orchid habitat depends on maintaining the hydrologic regime (U.S. Fish and Wildlife Service 1996). Further, understanding interspecific differences in gross root morphology, mycorrhizal associations and below-ground spatial and nutrient competition between neighboring species may be needed to fully describe the habitat needs of the western prairie fringed orchid (Jastrow and Miller 1993).

The logistic regression equation presented in this paper correctly classified 84% of 38 swales using 4 variables. By collecting data on the cover of just Baltic rush, which would take about 45 minutes, and entering it in the equation, a land manager could classify 66% of the swales in this ecoregion as either suitable or unsuitable as orchid habitat. The higher the estimated probability value (e.g., 0.99), the greater the probability the swale will support orchids (Norusis 1990). This technique can be used to prioritize sites for altering management activities such as treating leafy spurge, livestock grazing and prescribed burning. This technique also allows the identification of suitable habitat when attempting to expand an existing population or establish a new one, thus increasing the odds of successfully transplanting plants or germinating seeds on the new site (Holsinger and Gottlieb 1991).

Although this model is based on presence or absence of orchids, in reality, there is likely a spectrum of suitability that varies in time (Hof et al. 1999). Data from multiple years may increase our ability to model the capacity of the Sheyenne National Grassland landscape to support a metapopulation by assessing whether or not there are suitable, but unoccupied, swales that could be colonized by orchids. In the meantime, this model provides a valuable tool for evaluating potential orchid habitat in this ecoregion. In other ecoregions, or for other rare species, quantitative habitat data could be collected and used in developing similar models.

Table 6. Classification rates at each step of a forward step-wise logistic regression model based on 19 orchid and 19 non-orchid swales on the Sheyenne National Grassland. Classification rates were estimated using "leave-one-out" cross-validation (Efron and Tibshirani 1993).

Step	Variable[a]	Observed Swale type	Number predicted non-orchid	Number predicted orchid	Classification rate
1	JUBA	orchid	13	6	68.4
		non-orchid	7	12	63.2
		AVERAGE			65.8
2	STPA	orchid	14	5	73.7
		non-orchid	6	13	68.4
		AVERAGE			71.1
3	Mg	orchid	15	4	78.9
		non-orchid	4	15	78.9
		AVERAGE			78.9
4	ASM2	orchid	16	3	84.2
		non-orchid	3	16	84.2
		AVERAGE			84.2

[a] JUBA = *Juncus balticus* canopy cover (%); STPA = *Stachys palustris* canopy cover (%); Mg = soil magnesium (mg/l); ASM2 = 1992 August soil moisture (%) at a depth of 0-2 cm.

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Effect of fire on perennial grasses in central semiarid Argentina

DANIEL V. PELAEZ, ROBERTO M. BOO, MIRTA D. MAYOR, AND OMAR R. ELIA

Authors are professor and researcher, Departamento de Agronomía (UNS) and Comisión de Investigaciones Científicas (CIC); professor and researcher, Departamento de Agronomía (UNS) and Comisión de Investigaciones Científicas (CIC); professor, Departamento de Agronomía (UNS); research technician, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Departamento de Agronomía, Universidad Nacional del Sur, (8000) Bahía Blanca, Argentina.

Abstract

Fire is a key factor in the temperate semiarid region of central Argentina. The objectives of this work were to evaluate the effect of different fire intensities applied during different seasons under field conditions on the mortality of *Piptochaetium napostaense* (Speg.) Hack., *Stipa tenuis* Phil., and *Stipa gynerioides* Phil., 3 of the dominant grasses within the region and to determine their thermal death points in the laboratory. Ten plants of each species were exposed to low fire intensity (300–400°C), high fire intensity (500–600°C), and no fire (control) in April and December 1994, May 1995, and January 1996. Fire treatments were applied with a portable propane plant burner. The thermal death point was determined (during fall and spring) using the Wright's technique. Although mortality with high fire intensity was always higher than mortality with low fire intensity for all species, differences were not significant ($p > 0.05$). Pooling both treatments, the highest ($p < 0.05$) average mortality for *P. napostaense* (55%) and *S. tenuis* (85%) was observed after the May burn. Average mortality for *S. gynerioides* was similar ($p > 0.05$) for all burning dates. Only after the May burn, was average mortality of *P. napostaense* and *S. tenuis* higher ($p < 0.05$) than average mortality of *S. gynerioides*. The thermal death point was similar in all studied species. It was 65°C during the fall, and 68°C during the summer. This could explain, at least in part, similar mortalities (except after the May burn) between species and the date of burning found in this study.

Key Words: fire mortality, fire intensity, thermal death point, *Piptochaetium napostaense* (Speg.) Hack., *Stipa tenuis* Phil., *Stipa gynerioides* Phil.

Resumen

El fuego es un factor clave en la región semiárida templada del centro de Argentina. Los objetivos de este trabajo fueron evaluar los efectos de diferentes intensidades de fuego aplicadas en distintas épocas del año bajo condiciones de campo sobre la mortalidad de *Piptochaetium napostaense* (Speg.) Hack., *Stipa tenuis* Phil., y *Stipa gynerioides* Phil., 3 de las gramíneas dominantes en la región y determinar sus puntos de muerte térmica en el laboratorio. Diez individuos de cada especie fueron expuestos a baja intensidad de fuego (300–400°C), alta intensidad de fuego (500–600°C), y ausencia de fuego (control) en abril y diciembre de 1994, mayo de 1995 y enero de 1996. Los tratamientos de fuego fueron aplicados con un quemador portátil. El punto de muerte térmica fue determinado en otoño y primavera usando la técnica de Wright. En todas las especies, la mortalidad con alta intensidad de fuego fue mayor a la mortalidad con baja intensidad de fuego, pero las diferencias no fueron significativas ($p > 0.05$). Combinando ambos tratamientos, el mayor ($p < 0.05$) promedio de mortalidad para *P. napostaense* (55%) y *S. tenuis* (85%) fue observado después de la quema de mayo. El promedio de mortalidad de *S. gynerioides* fue similar ($p>0.05$) en todas las fechas de quema. Sólo luego de la quema de mayo, el promedio de mortalidad de *P. napostaense* y *S. tenuis* fue mayor ($p < 0.05$) que el promedio de mortalidad de *S. gynerioides*. El punto de muerte térmica fue similar en todas las especies estudiadas. El mismo fue de 65°C durante el otoño, y 68°C durante el verano. Esto podría explicar, al menos en parte, las mortalidades similares (excepto después de la quema de mayo) entre especies y fechas de quema encontradas en este estudio.

Death of perennial grasses following fire is usually attributed to heat. The likelihood of death of a whole plant will depend upon both the extent of injury to its component parts and which tissues are affected by the heat (Whelan 1995). Vascular plant tissues can be killed over a wide range of temperatures if the given temperature is maintained for the appropriate length of time (Wright and Bailey 1982). The lowest temperature that results in no survival after a fixed period of exposure, usually ten minutes, is referred as the thermal death point (Wright 1970). Combinations of temperature and exposure time have been used to measure death by heat in plants in relation to fire.

Characteristics such as temperature, intensity and duration, and season and frequency of fire have important effects on vegetation

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responses to fire (Gibson et al., 1990). Other factors such as phenological stage (Wright and Klemmedson 1965), amount of fuel per plant (Wright 1971), growth form (Wright 1986), localization of regrowth tissues (Whelan 1995), and climatic conditions after fire (Bunting 1985) can also modify the effect of fire on the mortality of perennial grasses.

Fire is a key factor in the Caldén District (Bóo 1990), a temperate, semiarid phytogeographic region of 40,000 km^2 in central Argentina (Cabrera 1976), commonly known as the Caldenal. Some studies have investigated the effect of controlled fires on grass species in the Caldenal (Lutz and Graff 1980, Busso et al. 1993, Bóo et al. 1996, Peláez et al. 1997). However, information on the effect of different fire intensities during different seasons of the year on mortality of individual grass species is lacking, and thermal death points are unknown. The objectives of this work were to evaluate the effect of different fire intensities applied during different seasons of the year on the mortality of *Piptochaetium napostaense* (Speg.) Hack., *Stipa tenuis* Phil., and *Stipa gynerioides* Phil. under field conditions, and to determine their thermal death points in the laboratory. The first 2 species are abundant in the Caldenal and preferentially eaten by cattle, whereas *S. gynerioides* is largely neglected (Bóo et al. 1993, Bontti et al. 1999), thus increasing in abundance under heavy grazing (Distel and Bóo 1995).

Study Area

The study area is located in the southeastern corner of the province of La Pampa (38°45'S, 63° 45'W), and comprises an area of 20 ha which has been closed to grazing since 1982 (Fig. 1). Vegetation, climate, and soil of the region have been described by others (INTA 1980, Bóo and Peláez 1991). The herbaceous layer is dominated by grasses such as *Piptocahetium napostaense* and *Stipa tenuis*. *Stipa gynerioides* and *Stipa speciosa* Trin. et. Rupr. are also abundant. The dominant woody species are *Prosopis caldenia* Burk., *Prosopis flexuosa* DC., *Condalia microphylla* Cav., and *Larrea divaricata* Cav.

Annual mean temperature is 15.3°C with June being the coldest month (7°C) and January (23.6°C) the warmest. Average annual precipitation is 344 mm, and is concentrated in the fall and spring. The annual water deficit is about 400 mm (Peláez et al. 1994).

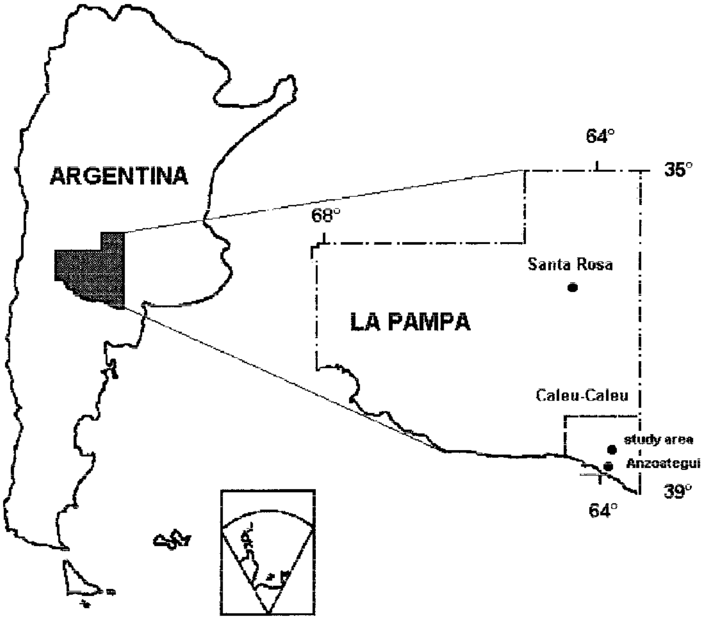

Fig. 1. Geographic localization of the study area. Department of Caleu-Caleu, province of La Pampa, Argentina.

The soil at the site is a Calciustoll, well drained with a medium to heavy texture. A petrocalcic horizon is found at an average depth of 40-60 cm (Peláez et al. 1997).

Materials and Methods

Mortality in the Field.

Individuals of *Stipa tenuis*, *Piptochaetium napostaense*, and *Stipa gynerioides* were randomly selected within the study area. Ten plants of each species were exposed to low fire intensity, high fire intensity, and no fire (control) in April and December 1994, May 1995, and January 1996.

Fire treatments were applied with a portable propane plant burner similar to the one described by Britton and Wright (1979). Low and high fire intensity treatments were obtained applying fire until the temperature in the crown had reached 300–400°C and 500–600°C, respectively. Temperatures were measured at 1 second intervals with a type K thermocouple (chromel-alumel) located at the soil surface level in the center of the plant without touching the soil or the plant, in the same way as reported by Bóo et al. (1996). Temperatures were recorded by connecting the thermocouples to a Campbell 21 XL datalogger. Further details regarding

Table 1. Mortality percentages of *Piptochaetium napostaense*, *Stipa tenuis*, and *Stipa gynerioides* treated with high fire intensity (HI), low fire intensity (LI), and no fire (CT). Treatment dates were April and December 1994, May 1995, and January 1996.

Date	Species	Mortality		
		HI	LI	CT
		(%)		
April ‘94	*P. napostaense*	20	0	0
	S. tenuis	10	0	0
	S. gynerioides	0	0	0
December ‘94	*P. napostaense*	10	10	0
	S. tenuis	40	10	0
	S. gynerioides	10	0	0
May ‘95	*P. napostaense*	60*	50*	0
	S. tenuis	90**	80**	0
	S. gynerioides	20	10	0
January ‘96	*P. napostaense*	10	0	0
	S. tenuis	0	0	0
	S. gynerioides	30	10	0

*,**significant at the 0.05 and 0.01 levels respectively.

Table 2. Basal diameter (n = 20) per plant for *Piptochaetium napostaense*, *Stipa tenuis*, and *Stipa gynerioides* in each burning date. In each row, values with the same letter are not significantly different ($p < 0.05$).

Date	Basal Diameter		
	P. napostaense	*S. tenuis*	*S. gynerioides*
	(cm)		
April ‘94	6.4 a	7.2 a	11.4 b
December ‘94	6.6 a	6.9 a	12.4 b
May ‘95	6.1 a	6.6 a	10.7 b
January ‘96	6.7 a	7.0 a	8.7 b

Table 3. Average mortality percentages (high and low fire intensity treatments pooled) of *Piptochaetium napostaense*, *Stipa tenuis*, and *Stipa gynerioides* after the April and December 1994, May 1995, and January 1996 treatments. In each column, values with the same letter are not significantly different ($p < 0.05$).

Date	Average Mortality		
	P. napostaense	*S. tenuis*	*S. gynerioides*
	(%)		
April ‘94	10 b	5 b	0 a
December ‘94	10 b	25 b	5 a
May ‘95	55 a	85 a	15 a
January ‘96	5 b	0 b	20 a

the burn techniques have been described by Peláez et al. (1997).

Surviving individuals of *S. tenuis*, *P. napostaense*, and *S. gynerioides* were counted at the end of the growing season following each fire. During each studied period and every 15–30 days, soil temperature (n = 10) and soil moisture (n = 10) at 10 and 30 cm of depth were determined using copper-constantan thermocouples and a gravimetric method (Wilcox 1951). Mortality data based on the number of individuals were analyzed using Chi-square (Snedecor and Cochran 1980).

Thermal Death Point and Evaluation

Duration of temperatures necessary to kill growing points of *Stipa tenuis*, *Piptochaetium napostaense*, and *Stipa gynerioides* were determined in 2 seasons of the year, summer and fall, following the technique described by Wright (1970). Summer and fall are the seasons with the highest occurrence of wildfires in the Caldenal. Fresh plants were randomly collected within the study site during April and December, 1997, and were kept in their sod prior to treatments. Culm bases (n = 6) 2.5 cm long and stripped of dead leaves were randomly selected from these plants. They were placed in dry stoppled test tubes and heated for various lengths of time in a constant temperature bath at 5°C intervals from 50 to 100°C. The culm bases were not placed in the test tubes until the air temperature within the test tubes was equal to the bath temperature. Temperatures within the test tubes were monitored with thermocouples connected to a Campbell 21 XL datalogger.

After each heat treatment, the culm bases were incubated at 30°C in continuous darkness for 15 hours in a 0.5% solution of triphenyl tetrazolium chloride to test viability. Growing points were considered dead only if absolutely no red or pink coloring was visible.

Results and Discussion

A significant mortality ($p < 0.05$) was only detected in *Piptochaetium napostaense* and *Stipa tenuis* ($p < 0.01$) after the May, 1995 treatments (Table 1). Although no statistical differences ($p > 0.05$) were found, field observations showed that mortality with the high fire intensity was slightly higher than mortality with the low fire intensity. This trend was similar in all the studied species (Table 1). These results partially agree with those reported by Bóo et al. (1996) who found that mortality of *P. napostaense*, *S. tenuis*, and *Stipa gynerioides* increased significantly ($p < 0.01$) with increasing fire intensity in most cases.

The high mortality, regardless of fire intensity, observed in *P. napostaense* and *S. tenuis* (Table 1) after the May 1995 treatment date can be explained by the severe drought that occurred during that year (Fig. 2), or by the combined effects of fire and drought. Becker et al. (1997) found that regrowth of *P. napostaense* and *S. tenuis* after defoliation was drastically affected by water stress. Peláez *et al.* (1997) found that fire reduced viability of axillary buds of *P. napostaense*, *S. tenuis*, and *S. gynerioides*, which in turn may restrict the subsequent regrowth. Availability of soil water during plant regrowth after fire appears to be more significant than direct fire damage (Redmann 1978). According to Whelan (1995), the interaction between fire and other ecological factors, such as herbivory and drought, has the potential to produce mortality

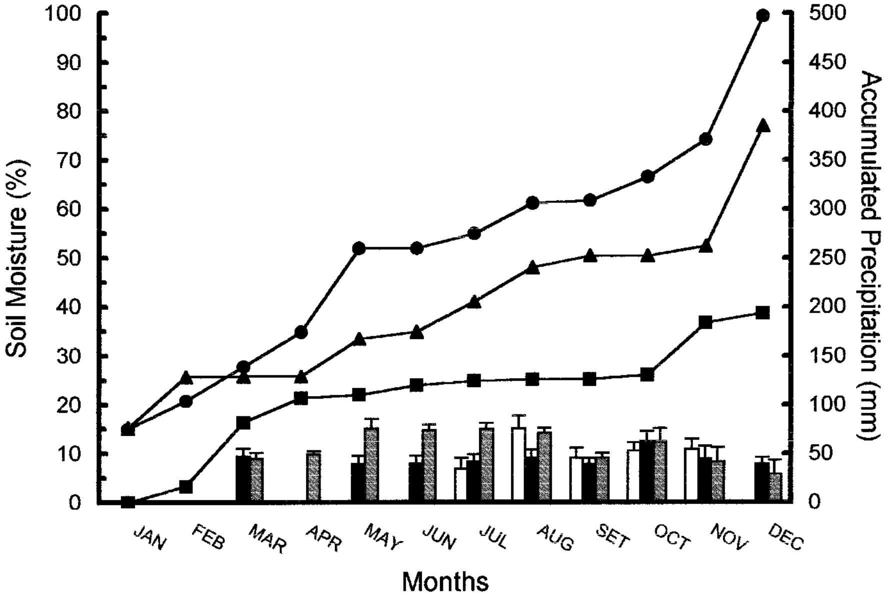

Fig. 2. Average soil moisture (%) between 10–30 cm in depth during each study period: 1994 ❑, 1995 ■, and 1996 ▨, and accumulated precipitation (mm): 1994 ▲, 1995 ■, and 1996 ●. Each column is the mean of N = 20, vertical bars represent mean standard deviations.

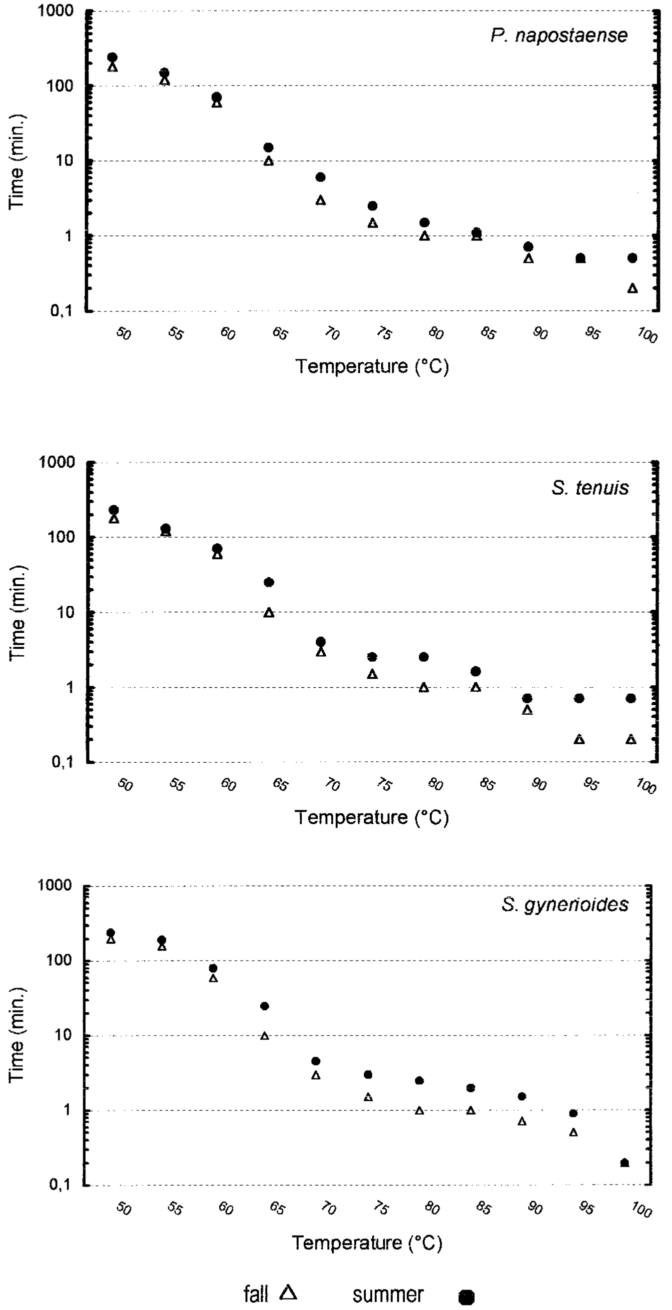

Fig. 3. Time required to kill growing points of *Piptochaetium napostaense, Stipa tenuis,* and *Stipa gynerioides* at different temperatures during 2 seasons of the year.

where fire alone would have had little impact. The reason for the much lower mortality observed in *S. Gynerioides* after the May 1995 treatment (Table 1) is a matter of speculation. A higher number of growing points per plant in this species due to the fact that the burned plants of *S. gynerioides* had a greater size ($p < 0.05$) than the burned plants of *S. tenuis* and *P. napostaense* (Table 2), could be a cause because some surviving plants of *S. gynerioides* had only a few active tillers after fire. On the other hand, the anatomical characteristics of the blades and stems of *S. gynerioides* (Metcalfe 1960, Lindström *et al.* 1998) would suggest that this species is very tolerant of water stress (Kramer 1983). On average, plants of *S. gynerioides* exposed to water stress grew more and had a higher number of new tillers than plants of *S. tenuis* (Busso personal communication). At least in part, the results obtained in our study would suggest that *S. gynerioides* is less susceptible to the combined effects of fire and drought than *P. napostaense* and *S. tenuis*.

The highest ($p < 0.05$) average mortality (pooling both treatments) for *P. napostaense* and *S. tenuis* was observed after the May burn (Table 3). Average mortality for *S. gynerioides* reached a maximum of 20% after the January burn but differences among burn dates were not significant ($p > 0.05$). When species' mortalities were compared within each burning date, only after the May burn was average mortality in *P. napostaense* (55%) and *S. tenuis* (85%) higher ($p < 0.05$) than in *S. gynerioides* (15%). This does not agree with results reported by Bóo *et al.* (1996) who found that mortality of *S. gynerioides* was higher than mortality of *P. napostaense* and *S. tenuis* after 1 accidental fire and 2 controlled fires. These differences might be due to different temperatures associated with different fuel loads reported by Bóo *et al.* (1996). They found heavier fuel accumulation and registered higher temperatures in the proximity of individuals of *S. gynerioides* than in the proximity of individuals of *P. napostaense* and *S. tenuis*. In our research temperatures were controlled, and the same for all species.

Several studies have emphasized the importance of season of fire on the mortality of perennial grasses. The importance of season has been related to moisture content (Wright 1971), phenological stage (Trollope 1984), and level of carbohydrate storage in plants (Wright and Klemmedson 1965). However, with the exception of the significant mortality found in *P. napostaense* and S. *tenuis* after the May 1995 burn, we did not find a significant ($p > 0.05$) number of dead plants after the other treatment dates (Table 1). Plants that are resting in a dehydrated state or at the beginning of the growing cycle can be more fire-tolerant than those that are metabolically active and fully hydrated (Anderson *et al.* 1970). This would partly explain the results obtained in our study because fire treatments were applied at the beginning (April and May) and at the end (December and January) of the annual growing cycle (Distel and Peláez 1985).

An inverse relationship was found between time and temperature combinations which proved to be lethal to the growing points of *P. napostaense*, *S. tenuis*, and *S. gynerioides* (Fig. 3). In all species for a given temperature, more time was necessary to kill the growing points during the summer than during the fall. Jameson (1961), Wright (1970) and Whelan (1995) reported similar results. This seasonal variation in heat resistance was in general attributed to changes in the moisture content of the plants. However, Wright and Bailey (1982) suggested that other factors such as content of pectin, lignin, salt, sugar, and density of plant tissue might be involved in the tolerance of plant tissue to heat.

The thermal death points of *P. napostaense*, *S. tenuis*, and *S. gynerioides* were similar. It was 65°C during the fall, and 68°C during the summer (Fig. 3). The thermal death point at the cellular level for herbage of average mesophytic plants usually lies between 50 and 55°C (Whelan 1995). However, Jameson (1961) found that lethal temperatures of culms for four grasses varied between 60 and 74°C. According to Wright and Bailey (1982), the widely quoted temperature of 60°C for one minute to kill plant tissue appears to be erroneous because the time to kill plants tissue at this temperature may vary from 2 to 60 min, depending on moisture content of tissues. Thus, the death of plant tissue is an exponential function between temperature and time if the moisture content is constant. In general, the results obtained in different studies would indicate a similar capacity of vegetal tissues to tolerate heat exposure among different grass species. Therefore, survival of plant exposed to intensive fire must be related to the protection of critical tissues from excessive heat exposure, and/or their metabolic activity at the time of fire. The similar thermal death points of *P. napostaense*, *S. tenuis*, and *S. gynerioides* would further indicate similar mortalities (except after the May treatment) between species and date of burn found in this study.

The effect of fire on mortality of perennial grasses depends on several environmental and biotic factors. A species that suffers high mortality in one fire may survive well in another, not because of plant factors, but because the fires and/or post-fire environmental conditions were different. Therefore, the final response of grasses to fire is the result of interactions among characteristics of the fire itself, processes that occur after fire such as climatic conditions and herbivory, and survival attributes of the plants in relation to the fire and to the post-fire processes.

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Autumn and spring drought periods affect vegetation on high elevation rangelands of Turkey

Ali KOÇ

Author is associate professor, Department of Agronomy, Faculty of Agriculture, Atatürk University, 25240 Erzurum, Turkey.

Abstract

The amount and temporal distribution of precipitation received is of critical importance for regrowth and plant production on rangelands. The effects of drought in the autumn, and spring/summer, as they affected sheep fescue (*Festucaa ovina* L.) dominated vegetation in Eastern Anatolia, Turkey, were examined between 1996 and 1998. Artificial drought was created using polyethylene rain-out shelters. The experiment was a randomized complete block design with 3 replications with a split-plot arrangement of treatments. Main plots included 2 autumn treatments: imposed artificial autumn-drought or a 40 mm of additional water plus rain. Sub-plots contained 4 treatments: artificial drought in May, June, July, or full spring rainfall. The number of reproductive shoots, aboveground biomass production, protein content, protein yield, canopy coverage and botanical composition were determined. Reproductive shoot numbers were reduced from 617 to 31 m^{-2} when plants entered winter without autumn regrowth as a result of autumn-drought. Plots subjected to drought in the autumn had aboveground biomass of 424 kg ha^{-1}. Protein content of forage, crude protein yield and water use efficiency (WUE) were 11.6%, 49 kg ha^{-1} and 1.5, respectively. These were compared with 1,038 kg ha^{-1}, 9.6%, 99 kg ha^{-1}, and 2.4, respectively, for plots received normal autumn precipitation in addition to 40 mm of additional water. Aboveground biomass production increased as short-term drought in spring was delayed but WUE was decreased. Autumn-drought had no effect on the proportion of grasses, but reduced legumes and resulted in an increase in other species. Spring/summer-drought had no effect on legumes but, as the onset of drought was delayed, grasses decreased and other species increased in composition. Autumn-drought reduced canopy coverage from 34.7% to 23.8% but spring drought had a negligible effect. Results indicated that autumn precipitation was crucial for productivity of these high elevation rangelands.

Key Words: *Festuca ovina*, water use efficiency (WUE), biomass, botanical composition, protein

Resumen

La cantidad y distribución temporal de la precipitación recibida es de importancia crítica para el rebrote y la producción de las plantas de los pastizales. Entre 1996 y 1998, al este de Anatolia, Turquía, se examino como la sequía en otoño y primavera/verano afectan la vegetación dominada por "Sheep fescue" (*Festucaa ovina* L.). Se creó una sequía artificial utilizando protectores contra lluvia hechos con polietileno. El experimento se condujo en un diseño de bloques completos al azar en parcelas divididas con tres repeticiones. Las parcelas principales incluyeron 2 tratamientos de otoño: 1. sequía de otoño impuesta artificialmente y 2. 40 mm de agua adicional mas lluvia. Las subparcelas contenían 4 tratamientos: sequía artificial en Mayo, Junio, Julio y la precipitación total de primavera. Se determinó el número de ramas reproductivos, la producción de biomasa aérea, el contenido y rendimiento de proteína, la cubertura de la copa y la composición botánica. Cuando las plantas llegaron al invierno sin rebrote de otoño como resultado de la sequía de otoño, el número de tallos reproductivos se redujo de 617 a 31 m^{-1}. Las parcelas sujetas a sequía en otoño tuvieron una biomasa aérea de 424 kg ha^{-1}. El contenido de proteína del forraje, el rendimiento de proteína cruda y la eficiencia del uso del agua (EUA) fueron: 11.6%, 49 kg ha^{-1} and 1.5, respectivamente. Estos valores se compararon con los de parcelas que recibieron la precipitación normal de otoño mas 40 mm de agua adicionales y que fueron: 1,038 kg ha^{-1}, 9.6%, 99 kg ha^{-1}, and 2.4, respectivamente. La producción de biomasa aérea aumento conforme se retrasó la sequía de periodo corto de primavera, pero la EUA disminuyó. La sequía de otoño no tuvo efecto en la proporción de zacates, pero redujo las leguminosas y resulto en un incremento de otras especies. La sequía de primavera/verano no tuvo efecto en las leguminosas, pero conforme se retrasó el final de la sequía, los zacates disminuyeron y otras especies incrementaron su composición. La sequía de otoño redujo la cobertura de la copa de 34.7% a 23.% y la sequía de primavera no tuvo efecto significativo. Los resultados indican que la precipitación de otoño fue crucial para la productividad de estos pastizales de alta elevación.

Most of 21 million ha rangelands of Turkey, occupying 28% of the total land area, occur in arid and semiarid areas. These rangelands are usually situated in the regions with elevations above 1,000 m and cool season plants such as sheep fescue (*Festuca ovina* L.) are dominant (Serin and Tan 1998). A paucity of precipitation restricts plant growth in these areas and forage production varies with fluctuations in climatic conditions (Herbel and Pieper 1991). The amount and temporal distribution of precipita-

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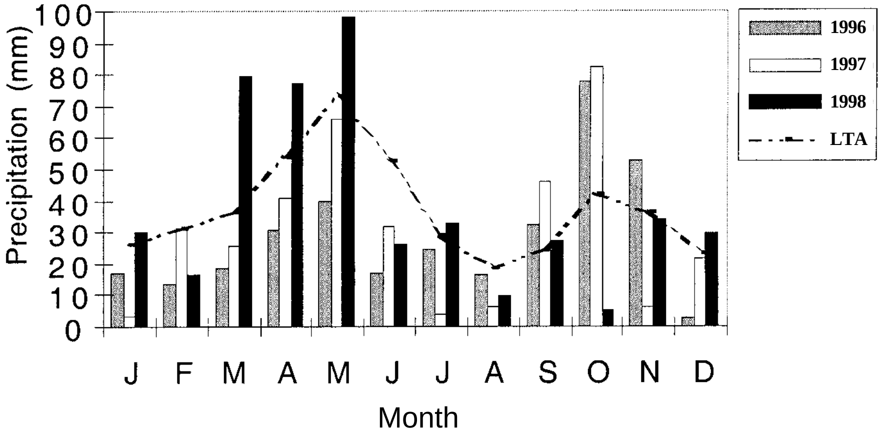

Fig. 1. Total monthly precipitation received during the experimental years and long term (1929–1998) average (LTA).

tion are the most important factors that affect water use efficiacy (WUE) and forage production (Le Houerou 1984). Precipitation received in the preceding autumn is critical for forage production (Walker et al. 1994), since cool season grasses require vernalization or short days for reproductive shoot development in arid areas where summer dormancy occurs (McDonald et al. 1996).

Drought not only reduces plant biomass and forage quality, but also alters species composition of rangeland vegetation. Under drought conditions, protein content of forage may increase as a result of a reduction in the fraction of stems to leaves produced (Peterson et al. 1992). Depending on the severity of drought, botanical composition may change and canopy coverage may also be reduced (Olson et al. 1985, Snyman and van Rensburg 1990, Snyman and Fouche 1993, Moldenhauer 1998).

Eastern Anatolia is the highest elevation (average 1,400 m) region in Turkey and more than half of its total area is rangelands (52.4%), making animal husbandry an important activity in the region (Gokkus and Koc 1996a). Eastern Anatolia's climate is semiarid with large fluctuations in precipitation within and between years. No work has been done on the effects of drought on biomass production in rangelands in Turkey. This study was undertaken to investigate the effects of drought during different periods (autumn or growing season) on the aboveground biomass, forage quality, botanical composition, canopy cover and WUE of vegetation.

Materials and Methods

This study was conducted on natural rangelands of Atatürk University, Erzurum, Turkey (39° 55' N, 41° 61' E with an elevation of 1853 m) between September 1996 and July 1998. The soil was sandy-loam with a neutral pH, low lime but rich potassium content. The soil was poor in phosphorous content with an organic matter content of 2.7% (Anon. 1998). The long term average yearly precipitation is 450 mm and the average annual temperature is 6°C. Precipitation during the experimental period is compared with long term average monthly precipitation in Figure 1.

Rangeland plants began spring growth in the last week of April and entered summer dormancy about the end of July, with growth ceased by lack of soil moisture. Plant regrowth occurs after the end of September when precipitation is received, or plants go directly into winter dormancy without shoot regrowth in the absence of precipitation (Koc 1995).

A randomized complete block design experiment with 3 replicates for 2 years was used in this study. A split-plot arrangement of treatments were used, with repeated measurement through 2 years. Main plots were 2 autumn treatments; artificial autumn-drought (a), and addition of 40 mm of supplemental water to support autumn regrowth (b). Autumn-drought main plots were covered with a clean polyethylene rain-out shelter which was open along each side to a height of 1 m above the ground to allow ventilation. These plots were covered between 15 September and 1 November to create artificial autumn-drought, while the other main plots received 40 mm of irrigation in addition to normal precipitation to enhance autumn growth. Supplemental water was applied once on 15 September in both years. Three of 4 sub-plots were sheltered from rain in either May (a), June (b) or July (c), and the other sub-plots received full spring rainfall (d). The total amount of water gained from precipitation and irrigation during the period between 15 September and 15 July in the experimental plots during the study years is presented in Table 1. Each sub-plot was 4-by-4 m. A 1-m buffer on each side was excluded from observation within each sub-plot.

When the dominant plant species, sheep fescue, was at the flowering stage, plant samples were taken by clipping two, 0.5 x 0.5 m areas within each sub-plot to soil surface. After the reproductive shoots were counted, litter and dead material were separated. The live plant material was oven dried at 100°C for 20 hours (Anon. 1987) to determine aboveground biomass. Total N content was analyzed using the Micro Kjeldahl method and crude protein content calculated by multiplying N content by 6.25 (Anon. 1987). Water use efficiency (WUE) was estimated as aboveground biomass (kg ha^{-1}) divided by total amount of water received an a sub-plot, including precipitation and irrigation, between 15 September and 15 July (Snyman and Fouche 1991).

Botanical composition and plant canopy coverage was determined each year using

Table 1. The amount of water (precipitation + irrigation or rain out) received on sub-plot during the experiment.

Year	Autumn Treatment	May drought	June drought	July drought	Rain fed
		Spring/summer treatment			
		------mm------			
1997	Drought	191	225	254	257
	Wet	330	364	394	396
1998	Drought	263	335	355	361
	Wet	430	502	522	528

the line intercept method (5 transects within each sub-plots, each being 2 m long). After determining the ratio of plant species, plants were grouped as grasses, legumes and other species. The other species group consisted primarily of forbs. Total canopy coverage was calculated as the ratio of the total plant intercepts to the total length of the transect (Tosun 1968).

An arc-sine transformation was used data for botanical composition and plant canopy cover. All data were subjected to analysis of variance based on general linear models for repeated measurements for a split plot arrangement of treatments using the MSTATC statistical package (Nissen 1983). Means were separated using Least Significant Difference (LSD) Test.

Results

There was no fall regrowth in autumn-drought plots, but grasses had 4-6 new leaves before the onset of the winter dormant period in autumn-wet plots in both years. An average of 617 reproductive shoots m^{-2} was produced when 40 mm of supplemental water was applied in the previous autumn. Only 31 tillers were produced when artificial autumn-drought was applied as compared with tillers when additional water was applied (Table 2). Spring/summer-drought timing had no significant effect on reproductive shoot number ($P > 0.05$). Shoot number was greater in the wetter year of 1998 than in 1997. No significant interaction effects among treatments occurred for reproductive shoot number.

Both autumn and spring/summer-drought significantly reduced aboveground biomass production ($P<0.01$). Autumn-drought reduced biomass production more than did spring/summer-drought (Table 2). The most severe reduction in production occurred if drought occurred in May. Thereafter, the effect of drought decreased as the onset of drought was delayed. Drought that occurred in July had no effect on production as compared with the rainfed treatment. Aboveground biomass was greater in wet year of 1998 than in 1997. There was no significant interaction among the treatments that affected aboveground biomass production.

Crude protein content was higher ($P < 0.01$) in the drier first year than in the secont year (Table 2). Crude protein content of the forage from the plots subjected to autumn-drought was higher ($P < 0.01$) than in other plots. Although artificial spring/summer-drought effects on crude protein content were insignificant, when data from both years were combined, crude protein content was higher in plant samples subjected to drought in June and July in the first year. But in the second year, crude protein content was higher for plants from the artificial May-drought treatment (Fig. 2). This may explain the year X spring-drought interaction effect ($P < 0.05$).

The effect of drought that occurred at different growth stages on crude protein yield was consistent with that of aboveground biomass production (Table 2). The differences were also significant ($P < 0.05$) in crude protein yield between the years, with greater protein yield in the wetter year.

Water use efficiency (WUE) was lower for plants in plots subjected to autumn-drought compared with plants for autumn-watered plots ($P < 0.01$), and there was no difference between years ($P > 0.05$). In spring, WUE was greater ($P < 0.05$) when May-drought was imposed than in other treatments. There was no significant interactions for WUE .

Grasses were affected more by spring/summer-drought and legumes were affected more by autumn-drought, while other species were affected by both autumn and spring/summer-drought (Table 3). Drought that occurred in May caused an increase in grasses ratio in the

Table 2. The effect of autumn- and spring-drought on reproductive shoot numbers, aboveground biomass, crude protein content, crude protein yield and WUE on high elevation rangeland vegetation in Turkey in 1997 and 1998.

	Spring/summer treatment				Year		
Autumn treatment	May drought	June drought	July drought	Rain fed	Average	1997	1998
Reproductive shoot number (Shoot m^{-2})							
Drought	28	28	29	40	31 b[1]	20	43
Wet	585	608	629	644	617 a	550	684
Average	307	318	329	342		285 b	363 a
Aboveground biomass production (kg ha^{-1})							
Drought	391	384	426	494	424 b	340	508
Wet	937	1039	1097	1079	1038 a	954	1122
Average	664 c	712 bc	762 ab	786 a		647 b	815 a
Crude protein content (%)							
Drought	11.5	11.6	11.7	11.6	11.6 a	12.0	11.2
Wet	10.0	9.3	9.8	9.3	9.6 b	10.3	8.9
Average	10.7	10.4	10.8	10.4		11.1 a	10.0 b
Crude protein yield (kg ha^{-1})							
Drought	45	44	49	56	49 b	41	57
Wet	93	96	107	100	99 a	98	100
Average	69 b	70 b	78 a	78 a		69 b	78 a
Water use efficiency							
Drought	1.7	1.3	1.4	1.6	1.5 b	1.5	1.5
Wet	2.5	2.4	2.4	2.4	2.4 a	2.6	2.3
Average	2.1 a	1.9 b	1.9 b	2.0 b		2.0	1.9

[1] Means with the same letters within a row or column for each parameter are not significantly different ($P > 0.05$).

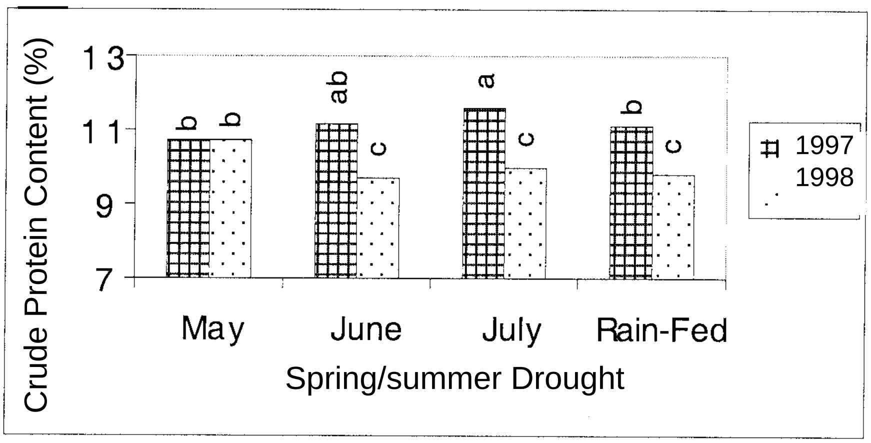

Fig. 2. Years x spring drought interaction effects on crude protein content. The columns with the same letters are not statisstically different (LSD, P < 0.05).

botanical composition ($P < 0.01$). The percentage of grasses was lower in the plots that were subjected to artificial drought in June with an autumn-drought as the main plots. However, grasses were lower in rain-fed sub plots of autumn-wet main plots, which resulted in significant ($P < 0.05$) interaction effects (Fig. 3). The percentage of legumes in the plots subjected to autumn-drought was 4.8%, but increased significantly ($P < 0.05$) to 9.6% when supplemental water was applied in autumn. Autumn-drought resulted in greater coverage of other plant species ($P < 0.01$). The coverage of these species increased from 16.3% to 23.4% as the drought was delayed in spring, but was similar between years. Interactions between autumn and spring/summer treatments were significant ($P < 0,05$). This resulted from an increase in the fraction of other plant species in the rain-fed sub plots of autumn wet main plots compared with other treatments (Fig. 4).

Autumn-drought significantly reduced plant canopy coverage ($P < 0.01$). Plant canopy coverage was 23.8% in the plots subjected to autumn-drought, but was 34.7% when supplemental water was applied in autumn. Spring/summer-drought periods had no effect on plant canopy coverage with no significant differences between years (Table 3). Interactions were also insignificant.

Discussion

Since rangeland ecosystems are located in arid and semiarid areas, precipitation is the most important factor that controls plant production in these ecosystems. Distribution of precipitation within a year is very important as is the total amount of precipitation. On high elevation rangelands, autumn precipitation had a great effect on plant production the following growing season in this study and in others (Walker et al. 1994). Plant production was related to the number of reproductive shoots produced in the preceding autumn. Reproductive shoot development in cool season grasses generally requires vernalization or short days (McDonald et al. 1996). Autumn moisture usually enhanced regrowth of reproductive shoots. Plants with low autumn reproductive shoot development produced vegetative shoots of varying height and sizes (Dahl 1995), which reduced total plant production and self regenerations of grasses. Our data showed that autumn drought resulted in considerable yield reductions.

Low aboveground biomass production when drought occurred in spring was related to lower leaf area, leaf number and shoot number, and depended on the intensity of stress (Busso and Richards 1995). As drought was delayed in the spring, reduction in aboveground biomass was associated with reductions in the effectiveness of precipitation, but depended on increases in ambient temperatures (Weltz and Blackburn 1995). Higher aboveground

Table 3. Effects of autumn- and spring-drought on plant composition and canopy coverage.

	Spring/summer treatment					Year	
Autumn treatment	May	June drought	July drought	Rain drought	Average fed	1997	1998
				Grasses (%)			
Drought	73.7	65.0	71.9	72.7	70.8	73.9	67.7
Wet	80.8	76.5	75.6	67.1	75.0	75.5	74.5
Average	77.2 a[1]	71.7 b	73.8 ab	69.9 b		75.1	71.1
				Legumes (%)			
Drought	3.2	6.8	5.3	3.7	4.8 b	5.8	3.8
Wet	9.8	9.2	9.9	9.5	9.6 a	8.8	10.4
Average	6.5	8.0	7.6	6.6		7.3	7.1
				Other species (%)			
Drought	23.1	28.2	22.8	23.6	24.4 a	20.3	28.5
Wet 9.4	14.3	14.4	23.4	15.4 b	15.7	15.0	
Average	16.3 c	21.3 ab	18.6 bc	23.5 a		18.0	21.8
				Total canopy coverage (%)			
Drought	23.4	23.2	25.4	23.4	23.8 b	24.0	23.7
Wet	34.2	34.6	35.5	34.6	34.7 a	34.7	34.8
Average	28.8	28.9	30.5	29.0		29.3	29.2

[1] Means with the same letters within a row or column for each parameter are not significantly different ($P > 0.05$).

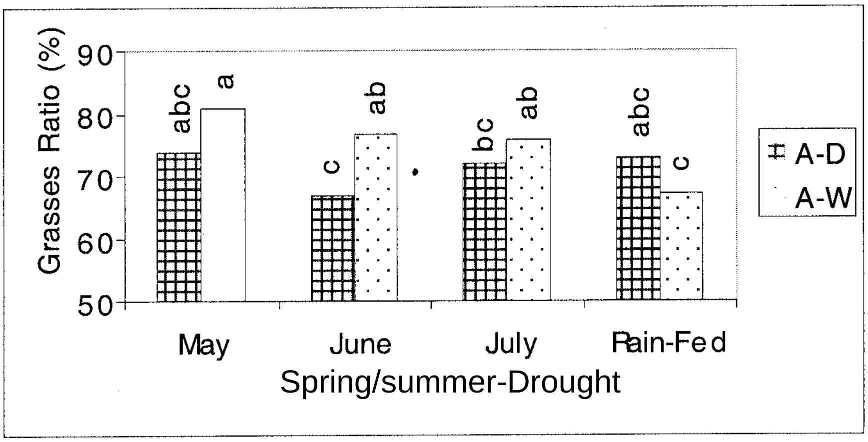

Fig. 3. Grasses ratio as affected by the interaction of autumn water regime and short growing season drought periods (A-D: autumn drought, A-W: autumn wet). The columns with the same letters are not statistically different (LSD, P < 0.05)

biomass production in the second year was related to higher precipitation received compared to that received in the first year (Table 1).

Autumn-drought caused an increase in crude protein content of forage that resulted from reduced reproductive shoot development. A higher fraction of stems reduces crude protein content (Gokkus and Koc 1996b). Higher crude protein content in the first year was related to lower precipitation received in that year and less stem growth. Drought retarded growth, but enhanced crude protein content (Peterson et al. 1992). Trends in crude protein yield paralleled those of aboveground biomass production. Higher crude protein yield of forage produced when drought occurred in the autumn did not, however, alleviate the loss in total protein yield (Table 2).

Water use efficiency (WUE) decreased in response to increasing intensity of drought (Le Houerou 1984, Snyman and van Rensburg 1990; Snyman and Fouche 1991). Relatively lower WUE was recorded for plants in plots subjected to drought in the autumn as compared with those where spring occurred. This probably originated from the failure of grasses to form reproductive shoots of high dry matter production potential. Higher ratios of vegetative shoots may lead to lower amounts of dry matter produced per unit of water lost. Therefore, autumn-drought may reduce WUE of rangeland vegetation.

Drought in the spring/summer, especially in May, was most important in reducing aboveground biomass production, but WUE was the highest in these treatments. Precipitation is normally high in May in the region (Fig. 1), which indicates higher rates of daily dry matter accumulation (Koc and Gokkus 1996). Lack of water during this early growth period caused a heavy yield penalty (Table 2). However, the soil water supply that accumulated over the winter was effectively used (Weltz and Blackburn 1995), resulting in higher rates of WUE. In other drought treatments in spring/summer, WUE was low despite higher aboveground biomass production. This might be associated with rapid evaporation of the precipitation received during June and July.

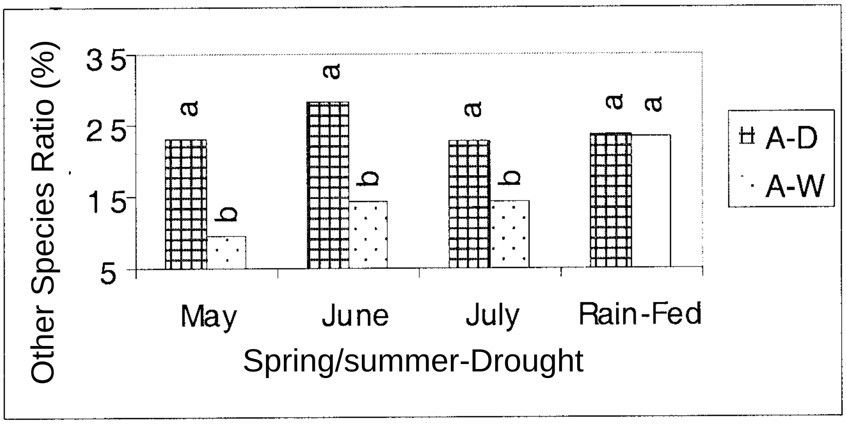

Fig. 4. Changes in the fraction of other species in relation to interaction of drought application period. The columns with the same letters are not statistically different (LSD, P < 0.05).

Drought that occurred in autumn probably led to a reduction in the amount of water stored in lower layers of soil. This could explain the lower proportion of legumes in the vegetation, because legumes are more sensitive to drought stress than are grasses (Haynes 1980).

Drought that occurred after May increased the proportion of plant species that belonged to other families. These species are often unpalatable (invader) plants. Another study also reported that invader species increased depending on drought conditions (Snyman and van Rensburg 1990). The decrease in the ratio of other species in the May drought period might be attributed to the failure of germination of annual weed seeds because of low soil moisture.

Autumn-drought reduced production of reproductive shoots of grasses and consequently canopy coverage was less as a result of lower basal diameter. This was consistent with observations by other workers (Snyman and van Rensburg 1990, Snyman and Fouche 1991, Walker et al. 1994, Koc 1995).

In conclusion, sufficient precipitation in autumn was the most important factor for fall regrowth that affected plant production the following year in high elevation rangelands. Drought that occurred in autumn severely affected aboveground production in these rangelands. Therefore, sufficient autumn precipitation is of vital importance for plant production. In these high elevation rangelands, drought after May was of little consequence for plant production. Precipitation received between September and May was, therefore, of critical importance.

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Book Review

Stolen Harvest: The Hijacking of the Global Food Supply. By Vandana Shiva. 2000. South End Press, Cambridge, Massachusetts. 146p. US$14.00 paper. ISBN 089608-607-0.

Vandana Shiva is not afraid to call a spade a spade. Her no-holds-barred approach to environmental issues is well known to people who have read her many books on the salient environmental wrongs of our times. In *Stolen Harvest*, Shiva fires the opening salvo on the very first page. We are told that "what the industrial economy calls "growth" is really a form of theft from nature and people" (p. 1). Shiva uses the 7 chapters of this book to tell an animated story of the effects of corporate agriculture on the environment, the lives of small farmers, and on the quality of the food we consume.

Chapter 1 focuses on the salience of seeds in promoting food security. It is noted that for most farmers, the seed is not only the source of future plants and food but also a repository of culture and history. In addition to this, the seed is the first link in the food chain. As such, it is essential that farmers be able to exchange seeds freely. This notwithstanding, because of the activities of certain corporations, it is becoming increasingly difficult to exchange seeds. As Shiva notes, centuries "of collective innovation by farmers and peasants are being hijacked as corporations claim intellectual-property rights on...seeds and plants" (p. 9). Although these points are well made, occasionally Shiva lets her zeal get the better of her. For instance, on p. 13, without any supporting evidence, she *claims* that while "the Green Revolution has been promoted as having increased productivity in the absolute sense, when resource use is taken into account, it has been found to be counterproductive and inefficient." Similarly, on p. 15, once again *without* any evidence, Shiva says that shrimp "cultivation destroys 15 jobs for each job it creates. It destroys $5 of ecological and economic capital for every dollar earned through exports." These numbers may well be accurate, but even so, it would be nice to know where Shiva got her information from.

In Chapter 2, Shiva discusses what she calls "soy imperialism" and the devastation of local food cultures. She points out that food security means having access to adequate food and "having access to culturally appropriatc food" (p. 21). The culturally appropriate cooking medium in vast parts of India is mustard oil. Yet, corporations such as Monsanto and others have made a concerted attempt to displace mustard with soybeans. As Shiva puts it, the Indian diet envisioned by the American Soybean Association "would be a monoculture of soybean, only its appearance would be diverse" (p. 31). The usefulness of these points is, once again, diminished by the presence of unsubstantiated claims. Here is an example. On p. 24, Shiva *claims* that the "link between dropsy and adulterated edible oil was first established by an Indian doctor in Bengal in 1926."

The subject of Chapter 4 is the boundary between species. Shiva tells us that a call to breach boundaries must not be made without first analyzing who gains and who loses from the breach of boundaries. She then goes on to note that industrial farming techniques tend to deprive varied species such as earthworms of their food sources. Further, to add insult to injury. these techniques destroy "the rich biodiversity in the soil and with it the basis for the renewal of soil fertility" (p. 62). The value of preserving biodiversity is repeatedly stressed in this book and this is certainly one of the book's strong points. Although Shiva's call to reverse what she calls the "McDonaldization" of the world is comprehensible, the same cannot be said about her quasi-romantic attitude toward the sacred cow in India. In fact, Shiva's prose in this part of the chapter sounds uncomfortably like the prose of Ashis Nandy and other defenders of tradition who hold that the quintessence of Indian national identity resides in Hindu traditions and that traditional female roles lie at the crux of the Hindu identity (see *Dominating Knowledge: Development, Culture, and Resistance* edited by S.A. Marglin and F.A Marglin, Oxford University Press, 1990).

In Chapter 5, the best chapter of this book, Shiva develops the idea that the tremendous diversity of crop varieties that have been developed by farmers over thousands of years is now "under threat from genetic erosion and genetic piracy" (p. 79). She notes that even though corporations misleadingly describe the consumption of packaged food as the food of the rich, what is in fact true is that in rich countries the wealthy eat fresh and not packaged food. As she puts it, it "is the poor who are forced to eat heavily processed or packaged food" (p. 87). Even though this is a very nice chapter, on occasion, Shiva is a little careless with her terminology. For instance, on p. 80, Shiva describes industrial agriculture as a corporate monopoly. However, the subsequent discussion on p. 81 clearly shows that this industrial agriculture is not a monopoly but an oligopoly.

Chapter 6 focuses on the nexuses between genetic engineering and food security. Shiva begins the proceedings by noting that the so called "life sciences" corporations "steal knowledge from citizens by stifling independent science and denying consumers the right to know what is in their food" (p. 95). Are genetically modified crops more expensive to cultivate than conventional crops? Shiva points out that because of higher seed, technology, and chemical costs, the answer to this question is yes. A noteworthy aspect of this chapter, and more generally this book, is that it successfully drives home the point that the systematically inferior position of women in most developing countries calls for the incorporation of gender as an important parameter in analyses of the effects of corporate agriculture on the lives of small farmers and on the quality of the food we consume.

In conclusion let me say that this is a lively book. Even though there are a few errors of commission and omission, the book contains a spirited attack on the evils of modern "life science" corporations such as Monsanto and Novartis. In addition, the book makes a good case for the conservation of biodiversity and it rightly highlights the unsavory effects of the activities of "life science" corporations on women in developing countries. As such it seems apposite to conclude by noting that even if readers do not rise to the book's clarion call to reclaim the stolen harvest, it is unlikely that they will be bored by perusing this book.—*Amitrajeet A. Batabyal*, Rochester Institute of Technology, Rochester, New York.

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