Journal of Range Management

TABLE OF CONTENTS: VOL. 56, NO. 2, March 2003

The Trail Boss

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

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INSTRUCTIONS FOR AUTHORS appear on the inside back cover of most issues. *THE JOURNAL OF RANGE MANAGEMENT* (ISSN 0022-409X) is published bimonthly for $56.00 per year by the Society for Range Management, 445 Union Blvd., Ste 230, Lakewood, Colorado 80228. PERIODICALS POSTAGE paid at Denver, Colorado and additional offices.

POSTMASTER: Return entire journal with address change—Address Service Requested to Society for Range Management, 445 Union Blvd., Suite 230, Lakewood, Colorado 80228.

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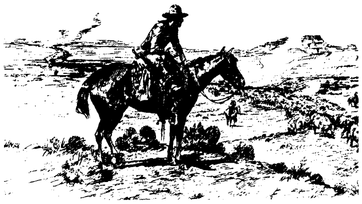

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—*to assist all who work with range resources to keep abreast of new findings and techniques in the science and art of range management;*

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

—*to create a public appreciation of the economic and social benefits to be obtained from the range environment;*

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J. Range Manage.
56: 106 -113 March 2003

State and transition modeling: An ecological process approach

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Abstract

State-and-transition models hold great potential to aid in understanding rangeland ecosystems' response to natural and/or management-induced disturbances by providing a framework for organizing current understanding of potential ecosystem dynamics. Many conceptual state-and-transition models have been developed, however, the ecological interpretation of the model's primary components, states, transitions, and thresholds, has varied due to a lack of universally accepted definitions. The lack of consistency in definitions has led to confusion and criticism indicating the need for further development and refinement of the theory and associated models. We present an extensive review of current literature and conceptual models and point out the inconsistencies in the application of nonequilibrium ecology concepts. The importance of ecosystem stability as defined by the resistance and resilience of plant communities to disturbance is discussed as an important concept relative to state-and-transition modeling. Finally, we propose a set of concise definitions for state-and-transition model components and we present a conceptual model of state/transition/threshold relationships that are determined by the resilience and resistance of the ecosystems' primary ecological processes. This model provides a framework for development of process-based state-and-transition models for management and research.

Resumen

Los modelos de estados-y- transición presentan un gran potencial para ayudar a entender la respuesta de los ecosistemas de pastizal a los disturbios naturales y/o inducidos por el manejo al proveer una estructura para organizar el conocimiento presente de las dinámicas del potencial del ecosistema. Muchos modelos conceptuales de estados-y-transición han sido desarrollados, sin embargo, la interpretación ecológica de los componentes principales del modelo: estados, transiciones y umbrales han variado debido a la carencia de definiciones universalmente aceptadas. La falta de consistencia en las definiciones ha conducido a confusión y critica indicando la necesidad de un mayor desarrollo y refinamiento de la teoría y los modelos asociados. Nosotros presentamos una revisión extensiva de la literatura actual y modelos conceptuales y puntualizamos las inconsistencias en la aplicación de los conceptos de la ecología de no equilibrio. La importancia de la estabilidad del ecosistema, definida como la resistencia y resilencia de las comunidades vegetales a los disturbios, se discute como un concepto importante relativo al modelaje de estados-y- transición. Finalmente, proponemos un grupo de definiciones concisas para los componentes del modelo de estados-y-transición y presentamos un modelo conceptual de las relaciones de estados/transiciones/umbrales que están determinadas por la resilensia y resistencia de los principales procesos ecológicos del ecosistema. Este modelo provee un marco para el desarrollo de modelos de estados-y-transición basados en procesos para manejo e investigación.

Key Words: state, transition, threshold, modeling, ecological, process

Applied ecology disciplines, such as range management, are necessarily organized around a response model based on theoretical supposition. Thus, the litmus test for an ecological or mechanistic model is its ability to predict the consequences of natural disturbances and/or management activities with acceptable precision over timescales relevant to management. Traditional theories of plant succession leading to a single climax community have been found to be inadequate for understanding the complex successional pathways of semi-arid and arid rangeland ecosystems considering timescales important for making management adjustments (West 1979, Westoby 1980, Anderson 1986, Foran et al. 1986, Tausch et al. 1993). After 50 years of applying the quantitative climax model of Dyksterhuis (1949) to rangeland management its predictive capabilities have come under scrutiny. The inability of the model to incorporate multiple pathways of change has led some ecologists to abandon the model completely (Wilson 1984, Smith 1988). The recognition of this inadequacy has generated a search for an alternative theory that more correctly reflects the observed dynamics of rangeland ecosystems. As many scientists were questioning the validity of the climax model, Westoby et al. (1989) developed a foundational discussion and conceptual model based on non-equilibrium ecology. Numerous scientists have utilized these concepts as a basis for the development of conceptual models of vegetation dynamics which incorporate multiple successional pathways, multiple

Authors wish to thank L.E. Eddleman, N.E. West, M. Westoby, W.A. Laycock, and G.L. Peacock for insightful review.
This article is submitted as Technical Paper No. 11874 Oregon Agricultural Experiment Station, Corvallis, Ore.
Manuscript accepted 8 Oct. 2002.

steady states, thresholds of change, and discontinuous and irreversible transitions (Archer 1989, Friedel 1991, Laycock 1991, Fuhlendorf et al. 1996, Stringham 1996, Rietkerk and Van de Koppel 1997, Davenport et al. 1998, Oliva et al. 1998, Petraitis and Latham 1999, Plant et al. 1999, West 1999, West and Young 2000, Stringham et al. 2001). However, the ecological interpretation of Westoby's model has varied due to a lack of universally accepted definitions of the key concepts. The lack of consistency in definitions has led to confusion and criticism indicating the need for further development and refinement of the theory and associated models (Iglesias and Kothmann 1997).

The USDA Natural Resources Conservation Service (NRCS) adopted the use of state-and-transition vegetation dynamics in describing rangeland ecological sites. The attempt to use this concept illustrated the inconsistency in the definitions and concepts. The NRCS recognizes the need for consistency in the application of the concepts (USDA 1997). For management to utilize the non-equilibrium ecological model the definitions of model objects must be succinctly stated and validated.

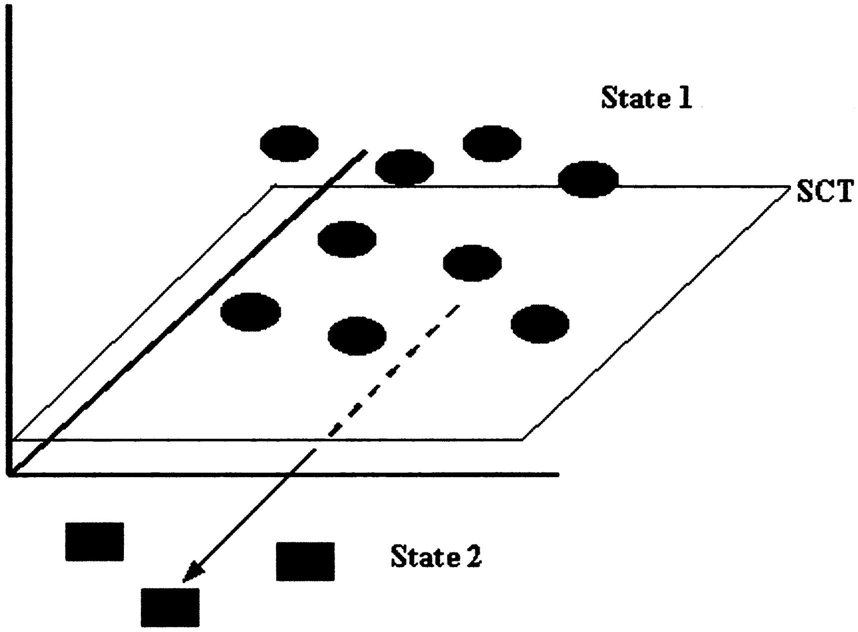

Fig. 1. Broad applications of the state-and transition concepts. Derived from the Society for Range Management, Task Group on Unity in Concepts and Terminology (1995). The plane labeled SCT (site conservation threshold) represents a change from 1 ecological site to another and may also be considered a threshold between 2 states. The individual boxes or ovals represent plant communities or seral stages that exist within 1 site.

Background

Westoby et al. (1989) was the first to apply the use of state-and-transition terminology to non-equilibrium theory for the purpose of producing a management focused model that describes vegetation dynamics in a non-linear framework as an alternative to the linear continuum process incorporated in the quantitative climax model. The authors defined a "state" as an alternative, persistent vegetation community that is not simply reversible in the linear successional framework. We interpret Westoby's transitions as trajectories between states with the characteristic of the transition being either transient or persisting. Transitions between states are often triggered by multiple disturbances including natural events (e.g., climatic events or fire) and/or management actions (grazing, farming, burning, etc.). Transitions may occur quickly, as in the case of catastrophic events like fire or flood or slowly over an extended period of time as in the case of a gradual shift in weather patterns or repeated stresses like frequent fire. Regardless of the rate of change the system does not stabilize until the transition is complete.

Quantitative approaches to ecological thresholds have been presented by May (1977), Wissel (1984) and Rietkerk and van de Koppel (1997). Archer (1989) introduced the qualitative concept of a transitional threshold. He modeled the expansion of a woodland community into a grassland domain using a transitional threshold as the boundary between the respective grassland and shrub domains. Whisenant (1999) proposed a model of degradation based on the stepwise degradation concept of Milton et al. (1994). Whisenants model is similar to Archer's, which incorporates 2 transition thresholds, the first being controlled by biotic interactions and the second by abiotic limitations. The concept of a transitional threshold as used by both Archer and Whisenant is similar to the persistent transition as the successional processes shift from grass controlled to shrub controlled, however, in Whisenant's (1999) model the focus is on ecological processes not vegetative groups. Friedel (1991) focused on the concept of thresholds of environmental change between domains of relative stability. She defined a threshold as a boundary in space and time between 2 domains or states, which is not reversible on a practical time scale without substantial inputs of energy. As defined, Friedel's thresholds mirror Westoby et al.'s (1989) definition of persistent or irreversible transitions. However, the use of thresholds in current state-and-transition models has not been consistent nor clear on whether thresholds exist between all states or only a subset of states.

Conceptual models, based on these ideas, have incorporated states and transitions but not always thresholds. As a result, there have been both a broad interpretation of states, more or less separated by thresholds, and a narrow interpretation of states that approximate seral stages or phases of vegetation development. Broadly applied, states are climate/soil/-vegetation domains that encompass a large amount of variation in species composition. Specifically a grassland state would include many seral stages of the overall grassland community. These seral stages are within the amplitude of natural variability characteristic of the state and represent responses to disturbances that do not force a threshold breach. Westoby et al. (1989), Archer (1989), and Archer and Smeins (1991) provided examples of this broad definition of state where domination of successional processes determine the boundary of the state (e.g. grass controlled succession versus shrub controlled succession). The Society for Range Management, Task Group on Unity in Concepts and Terminology (1995) developed a graphical depiction of the broad application of states with multiple vegetative stages diagrammed within one state (Fig. 1). Milton et al. (1994) and Whisenant (1999) de-emphasized the species component of the ecosystem within their models, focusing instead on the functional integrity and self-repair thresholds of the site for determining state boundaries. In the broad definition of state the natural variability characteristic of plant communities within a site is the result of, and contributes to, the current functional integrity of the site's primary ecological processes (hydrology, nutrient cycling, and energy capture).

The narrower interpretation of state allows for far less variation in plant community composition. States are typically depicted as seral stages or phases of vegetation development. In the narrow application of the model a state change does not necessarily represent a movement across a threshold as envisioned by Friedel (1991). Figure 2 represents the narrow interpretation of states as adapted from West (1999). Boxes represent states and arrows indicate the transitions between states. Note that many of the transitions are reversible, however, the threshold indicates a persistent transition. Other examples of specific or narrow applications of states are presented by Weixelman et al. (1997), Oliva et al. (1998), Allen-Diaz and Bartolome (1998), West (1999), and West and Young (2000). The specific approach to state-and-transition modeling may be the reason for statements that such models are structurally similar to traditional linear climax-seral stage models. The significant difference being the description of communities as discrete entities as opposed to the continuum concept of the quantitative climax model (Iglesias and Kothmann 1997).

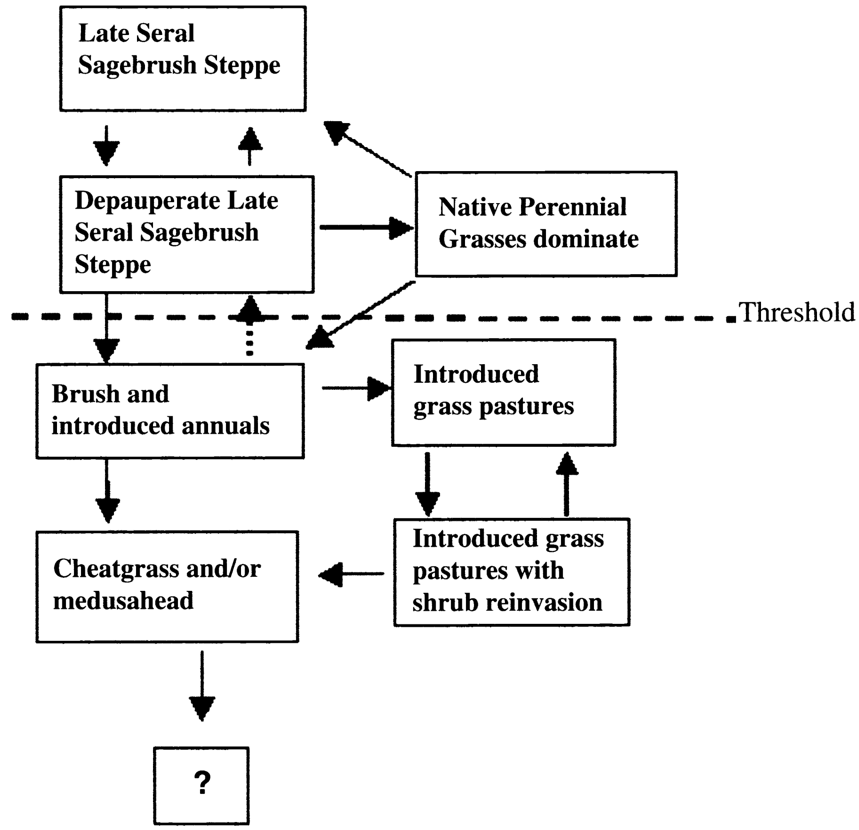

Fig. 2. Specific, or narrow, application of states with each state (box) representing 1 phase or seral stage of vegetation development. Transitions between states are indicated by arrows and the dashed line represents a threshold. The dashed transitional line signifies the requirement of substantial energy input to move the state back across the threshold. Modified from West (1999) and West and Young (2000).

Ecological Resistance and Resilience

The concept of stability as defined by the resistance and resilience of plant communities have been discussed in the literature for sometime and offer important insights for state-and-transition models (Margalef 1969, Verhoff and Smith 1971, Holling 1973, May 1977, Noy-Meir and Walker 1986). Resistance is defined as the ability of the system to remain the same while external conditions change whereas resilience is the ability of the system to recover after it has been disturbed. Thus, fully functioning ecosystems are both resistant to change and resilient or able to recover without external energy inputs thereby maintaining stability while allowing for fluctuating combinations of plant species over time. States, by definition are relatively stable (Westoby et al. 1989), therefore it follows that a state change is only possible when a threshold is crossed. Accepting this concept points out the confusion that is apparent in the current attempts to produce state-and-transition models. The specific or narrow approach has produced models, which depict state changes occurring without having crossed a threshold. Often such changes are diagrammed as reversible and perhaps occur without the input of management resources (Fig. 2). Rather than consider these vegetation dynamics as state changes it is more appropriate to consider them as phase shifts or plant community dynamics within a state. Therefore, within a state there exists the potential for a large variation in species composition, which is merely a reflection of plant community dynamics. A state change, on the other hand, requires a shift across a boundary or threshold, defined by a change in the integrity of the site's primary ecological processes, resulting in a different potential set of plant communities.

Rangeland Ecological Processes

Ecological processes functioning within a normal range of variation will support a suite of specific plant communities. The important primary processes are (1) hydrology (the capture, storage, and redistribution of precipitation); (2) energy capture (conversion of sunlight to plant and animal matter); and (3) nutrient cycling (the cycle of nutrients through the physical and biotic components of the environment (Pellant et al. 2000, Whisenant 1999). Pellant et al. (2000) defines the functioning of an ecosystem by "the degree to which the integrity of the soil, vegetation, water, and air, as well as the ecological processes of the rangeland ecosystem, are balanced and sustained". Integrity is defined as the "maintenance of the functional attributes characteristic of a locale, including normal variability" (Pellant et al. 2000). Degradation of an ecosystem occurs when the integrity of the system is damaged or lost. Maintenance of a functional site or repair of a damaged site requires management focused on soil stability, nutrient cycling, and the capture, storage and safe release of precipitation. Vegetation goals should be based on the concept of vegetation as a tool for maintaining or repairing damaged ecological processes rather than predefined species groups. Monitoring of species groups may be a mechanism for evaluating or detecting change in the site's ecological processes.

Clarification of the Concepts and Definitions

Spatial Scale

Ecosystems are difficult to define or delimit in space and time. Hierarchy theory, as applied to ecological systems, suggests several levels of organization exist, i.e., organisms, populations, communities, ecosystems, landscapes (Archer and Smeins 1991). Each level of organization encompasses one or more of the primary ecological processes that are operating at specific spatial and temporal scales. Although landscape scale management may be the goal, our current understanding of organization function declines with increasing spatial and temporal scale.

The ecological site concept has long been utilized as an organization level that provides an appropriate spatial scale for inventory, evaluation, and management of rangelands (USDA 1997). Organisms, populations, and communities exist within this spatial scale and interact with one another through the flow of water and energy, and the cycling of nutrients. An ecological site has evolved a kind of characteristic plant community such as cool season shrub-grass or warm season grassland. Within an ecological site numerous expressions of the various developmental stages of the characteristic plant community can occur. The concept and definition of an ecological site fits the large-scale interpretation of the state-and-transition model. We define the ecological site as the minimum scale for definition of a state.

Temporal Scale

The definition of threshold as presented by Friedel (1991) indicates that once a threshold has been breached return to the previous state is precluded within a time frame relevant to management, without substantial inputs of energy. Ecological management models should focus on the time required to repair damaged ecological processes not on a time scale predicated by management. Careful consideration of the threshold concept negates the need for including management timescales in the definition of ecological thresholds as these thresholds represent a permanent change in the function of the state. Thus, restating the threshold definition, independent of management timescales, results in the conclusion that once a threshold has been violated return to the prior state is precluded without substantial inputs of energy. Therefore, under the current climatic conditions and without substantial inputs of energy, state changes are permanent. The temporal scale is defined by the permanence of the current climate regime.

State

A state is a recognizable, resistant and resilient complex of 2 components, the soil base and the vegetation structure. The vegetation and soil components are necessarily connected through integrated ecological processes that interact to produce a sustained equilibrium that is expressed by a specific suite of vegetative communities.

Soil Base and Vegetation Structure

The base of any rangeland ecosystem is the soil resource that has developed through time from a specific parent material, climate, landscape position, and interaction with soil and terrestrial biota. These factors are the primary determinants of the ecological site's capability. The integrity of the soil resource, as reflected by site hydrology and nutrient cycling, is directly connected to the composition and energy capture process of the above-ground vegetative component. The interaction between the soil resource and the associated vegetative community determines the functional status of the state's ecological processes.

- Soil Base: a component that results from the interaction of climate, abiotic soil characteristics, soil biota and topography that determines the hydrologic characteristic and biotic potential of the system.
- Vegetation Structure: a component resulting from above ground communities of living organisms, whose vital attributes (Noble and Slatyer 1980) competitively capture and utilize the system's available energy, water, nutrients, and space.

The interaction between the structural attributes of soil and the vegetative communities, through the processes of energy capture, hydrology and nutrient cycling defines the resilience and resistance of the state.

Resilience and Resistance

The stability of a state is defined above in terms of resilience and resistance. Resilience and resistance are inherent properties of an ecosystem that are determined by the physical components of the system and the functional capacity of the associated ecological processes. Resilience focuses on how far a system can be displaced from equilibrium before return to equilibrium is precluded. The emphasis is placed on the persistence of relationships as they affect the systems ability to adapt to change (Walker et al. 1981), therefore, resilience relates to the functioning of the system's ecological processes. Resistance indicates the ability of a system to remain at or near its equilibrium condition by maintaining control of its ecological processes. Thus, the strength of this control determines a system's inherent resistance to change. Consequently, under an existing climate, stability of a state is a function of the combination of its inherent resilience and resistance.

Thresholds and Transitions

Thresholds are points in space and time at which one or more of the primary ecological processes responsible for maintaining the sustained equilibrium of the state degrades beyond the point of self-repair. These processes must be actively restored before the return to the previous state is possible. In the absence of active restoration a new state, which supports a different suite of plant communities and a new threshold, is formed

- Thresholds: boundary in space and time between any and all states, or along irreversible transitions, such that one or more of the primary ecological processes has been irreversibly changed and must be actively restored before return to a previous state is possible.

Transitions are trajectories of change that are precipitated by natural events and/or management actions which degrade the integrity of 1 or more of the states primary ecological processes. Transitions are often composed of 2 separate properties that are defined by the state threshold. The first property is reversibility and it occurs within the state. The second property is irreversibility and it occurs once a threshold has been breached. Transitions are vectors of system change that will lead to a new state without removal of the stressor(s). The primary difference between the reversible and irreversible property of a transition is defined by the systems' ability or inability to repair itself.

• Transition: a trajectory of system change away from the current stable state that is triggered by natural events, management actions, or both.

– Reversible Property of the Transition: trajectory of change that occurs within a state and indicates the system is moving toward a threshold. Reversal requires elimination of the stress or stresses responsible for triggering the transition.

– Irreversible Property of the Transition: trajectory of change that occurs after a threshold has been breached. The system can no longer self-repair even with removal of the stressor(s). The system will not come to rest until a new equilibrium (i.e., new state) is established that supports a different suite of plant communities.

Model Structure

The conceptual model, illustrating the above definitions, is represented in Figures 3 and 4. The model accommodates both the quantitative climax approach and the narrow application of the non-equilibrium approach to states and transitions (Fig. 5). States are diagrammed as the large boxes and are bordered by thresholds. Thresholds are the boundaries of any and all states, but may also occur during the transition between states. For a state change to occur a threshold must be breached. The small boxes within the state are referred to as plant community phases or seral stages and are joined by community pathways that flow in both directions. Transitions are reserved for a trajectory of change with the dashed line inside the state indicating the portion of the transition that is reversible with minimal input from management. Figure 4 illustrates the process of a state change. Once the threshold is crossed the state has lost control of its primary ecological processes, is no longer able to self-repair and will transition to a new equilibrium with a different ecological capability. The entire trajectory from a vegetation phase in State 1, across the threshold to the formation of State 2 is considered a transition and represents a degradation of ecological capability. The portion of the transition contained within the boundary of State 1 is reversible with removal of the stressor(s), however, once the trajectory crosses the threshold it is not reversible without active restoration including substantial energy input. Additional thresholds may occur while the system is in transition, changing the direction of the trajectory away from State 2 towards State 3 (Fig. 4). State-and-transition modeling efforts indicate the first threshold is forced by a change in the biotic component of the system whereas additional thresholds would involve changes in the soil resource (Westoby et al. 1989, Milton et al. 1994, and Whisenant 1999).

Plant community phase changes within states, in addition to transitions of change, thresholds and multiple stable states are illustrated in Figure 5. The management and natural mechanisms responsible for community phase shifts and transition initiation must be defined in terms of ecological processes and included in the model description. For example, prolonged drought or overgrazing leads to a reduction in the perennial herbaceous understory. The decrease in perennial understory leads to a decrease in total energy capture and nutrient cycling. In addition, the plant community's ability to protect the soil from raindrop impact and potential soil erosion declines. The mechanism (or mechanisms) of disturbance have led to a change in the 3 primary ecological processes and a phase shift as diagrammed by community phase pathway P1 (Fig. 5). In the case of prolonged drought return to the late seral sagebrush steppe phase would gradually occur with a return to a normal or above normal precipitation period (P2). Increased available moisture leads to an increase in biomass of the herbaceous understory that translates into an increase in energy capture, nutrient cycling and an improvement in soil protection and site hydrology. The degradation mechanism of overgrazing would need to be addressed through grazing management with the goal of improving the function level of the primary ecological processes. Continued overgrazing would further decrease the vigor of the native herbaceous understory and further impact the community's ability to maintain control of the primary ecological processes. As the vigor of the native

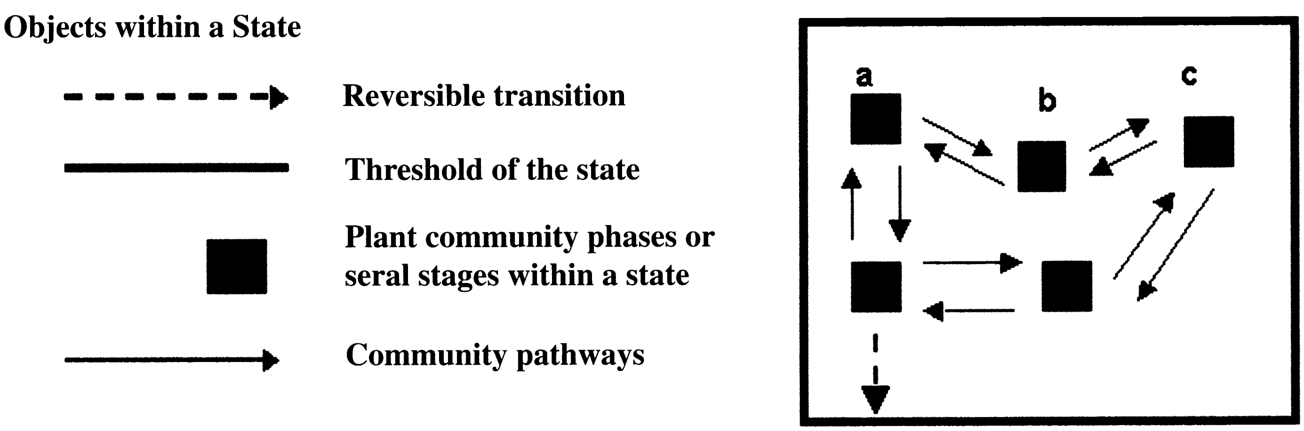

Fig. 3. Conceptual model depicting the objects of 1 state. Note the linear response, retrogression-succession model may be modeled within the state (i.e., a to b to c and vice-versa).

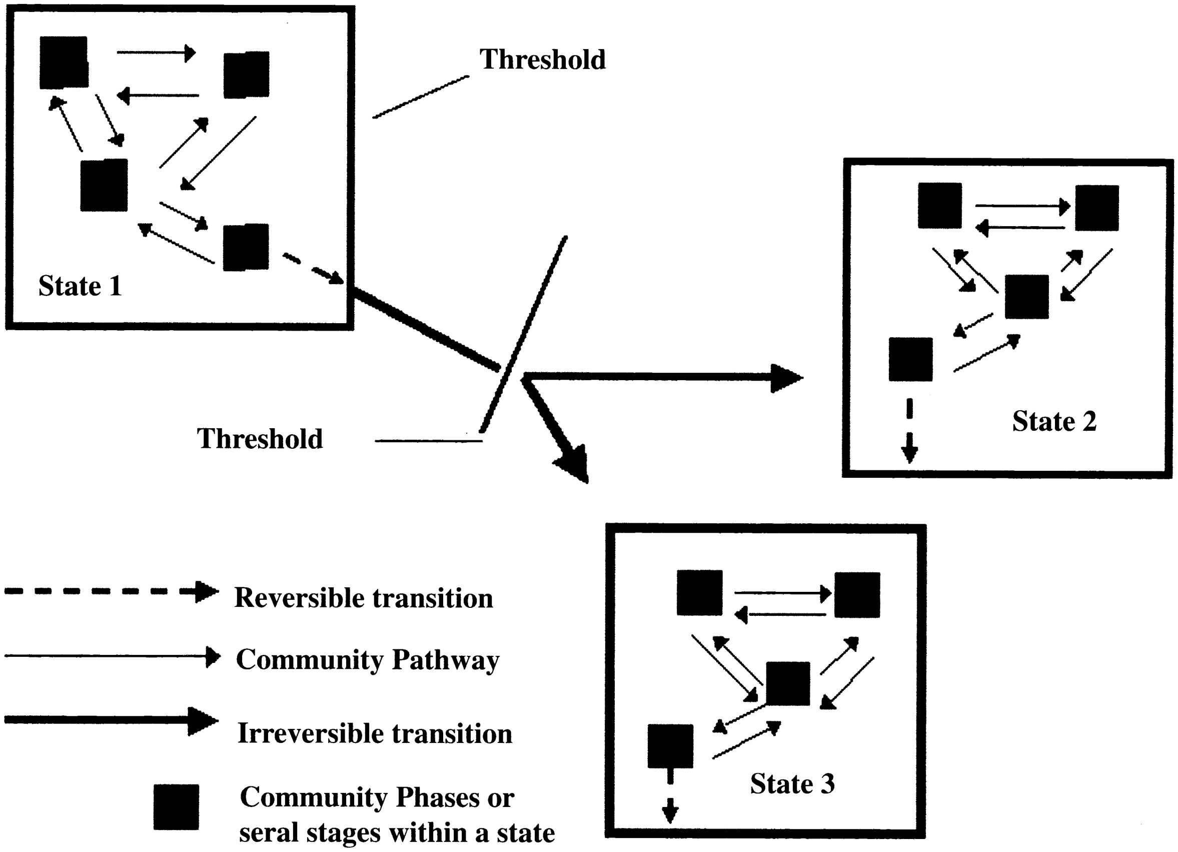

Fig. 4. Conceptual state-transition model incorporating the concepts of community pathways between plant community phases within states, reversible transitions, multiple thresholds, irreversible transitions, multiple pathways of change, and multiple steady states.

herbaceous community declines, the site is opened up for invasion by annual species. The transition from State 1 towards State 2 has begun and will continue without the removal of the stress from improper grazing (T1a). At the point in time where annuals dominate the herbaceous understory and fire frequency intensifies, the state has crossed a threshold and is transitioning to a new state (T1b). During this transition phase the plant community may still retain a minor component of sagebrush; however, this is not representative of a stable state and with increased fire frequency the brush will be eliminated and the new equilibrium state formed. The new state is defined as a *Bromus tectorum* (cheatgrass) and/or *Taeniatherum asperum* (medusahead) dominated community with a fire frequency interval of 2 to 3 years. Energy capture has declined and the time period for energy capture has been reduced. Nutrient cycling in both the vertical and horizontal plane has decreased with the shift to a shallow rooted, primarily monoculture community. The hydrology of the site will be impacted through a reduction in the amount of organic material being added to the soil and an increase in the potential for damage to soil surface structure from raindrop impact. Return to State 1 would be impossible without the use of intensive management inputs. The practicality of this level of management would preclude its use. State 3 may be the practical state of choice.

Although many scientists have recognized the short-comings of the quantitative climax model developed by Dyksterhuis (1949) there are ecosystems, generally of more mesic climates, where the linear model is appropriate. It is important to realize that any modeling approach is a best-fit solution, not a perfect-fit solution. Therefore, the retrogression-succession continuum can be modeled within the states to depict the situation where plant community phases do respond linearly. However, it is also possible for linear response mechanisms to be pushed past an ecological threshold, resulting in a state change.

Conclusions

Definitions and model concepts as discussed in this paper are being adopted by the USDA Natural Resources Conservation Service as the standard for describing vegetation dynamics in rangeland ecological site descriptions. State-and-transition models hold great potential to aid in understanding rangeland ecosystems' response to natural and/or management-induced disturbances by providing a framework for organizing understanding of potential ecosystem dynamics. Many state-and-transition model applications are available in the literature, although the scale of interpretation of the concepts has varied. We have attempted to review and clarify a large amount of information into a proposed conceptual model of state/transition/threshold relationships that are determined by the resilience and resistance of the systems' primary ecological processes. Most of the components presented are not new; however, the proposed model attempts to clarify the definitions

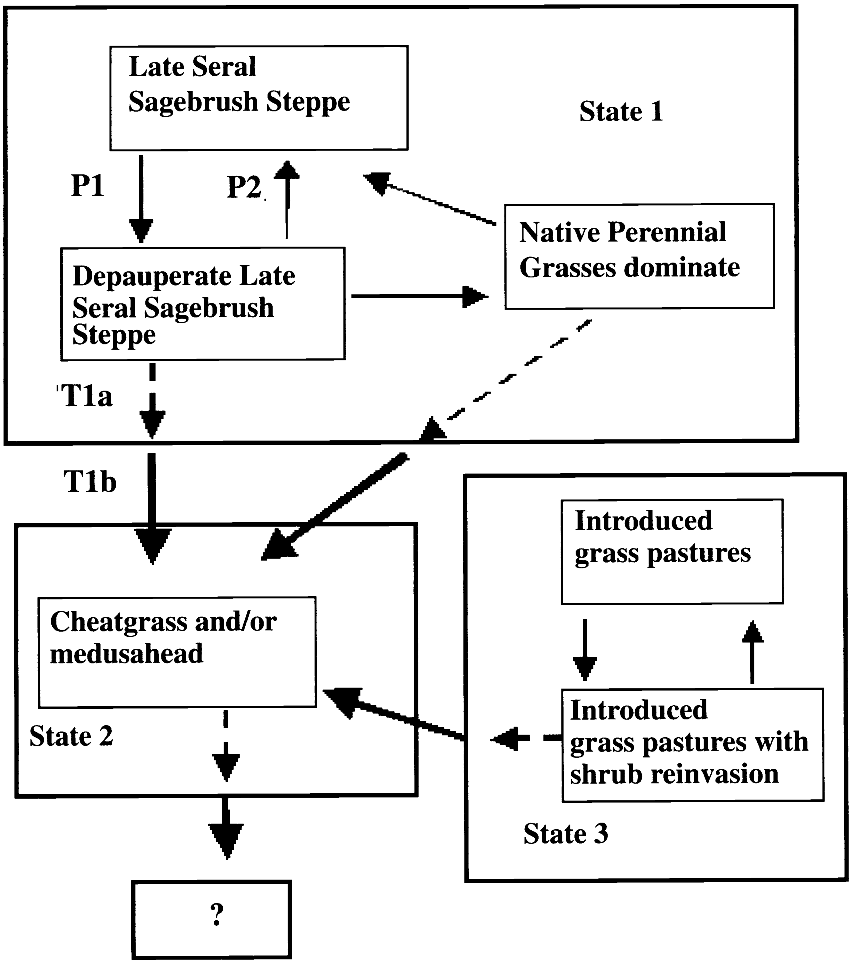

Fig. 5. Modification of the West (1999) and West and Young (2000) specific sagebrush steppe model (see Fig. 2) to illustrate the broad concept of state with plant community phases and community pathways (i.e., P1 and P2) within states. T1a and T1b signify the reversible and irreversible properties of the transition between State 1 and State 2. For additional discussion of the mechanisms leading to community phase shifts see West (1999) and West and Young (2000).

and concepts and to link them together into a process-based model for management and research. The management and natural mechanisms responsible for community phase shifts and transition initiation must be included in the model description. The description of these mechanisms should contain information on their impact on the primary ecological processes and the resulting change in the biotic community and system function. Further research is needed to identify indicators of change for ecological processes that will allow management to intervene prior to a threshold change. Once a threshold has been crossed, the focus of management should be on restoration of the damaged ecological processes, not on reestablishing a specific plant community. Although this conceptual model suggests that the ecological site is the minimum scale associated with a state, understanding ecological processes at the landscape scale should be the target. This model contains the flexibility to accommodate landscape level dynamics; however, further research is needed to clarify the ecological relationships occurring at that scale. This effort is not viewed as completed, but rather as another step in the process to further develop understanding of rangeland ecosystems.

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J. Range Manage.
56: 114-126 March 2003

Development and use of state-and-transition models for rangelands

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Abstract

State-and-transition models have received a great deal of attention since the introduction of the concept to range management in 1989. Nonetheless, only recently have sets of state-and-transition models been produced that can be used by agency personnel and private citizens, and there is little guidance available for developing and interpreting models. Based upon our experiences developing models for the state of New Mexico, we address the following questions: 1) how is information assembled to create site-specific models for entire regions, 2) what ecological issues should be considered in model development and classification, and 3) how should models be used? We review the general structure of state-and-transition models, emphasizing the distinction between changes among communities within states (pathways) that are reversible with changes in climate and "facilitating practices" (e.g. grazing management), and changes among states (transitions) that are reversible only with "accelerating practices" such as seeding, shrub control, or the recovery of soil stability and historical hydrologic function. Both pathways and transitions occur, so these models are complementary. Ecological sites and the climatically-defined regions within which they occur (land resource units) serve as a framework for developing and selecting models. We illustrate the importance of clearly delineating ecological sites to produce models and describe how we have dealt with poorly-delineated sites. Producing specific models requires an understanding of the multiple ecological mechanisms underlying transitions. We show how models can represent and distinguish alternative and complementary hypotheses for transitions. Although there may be several mechanisms underlying transitions, they tend to fall within discrete categories based upon a few, fundamental ecological processes and their relationships can be readily understood. A knowledge of mechanisms is closely related to the use of ecological indicators to anticipate transitions. We conclude that models should include 1) reference values for quantitative indicators, 2) lists of key indicators and descriptions of changes in them that suggest an approach to a transition, and 3) a rigorous documentation of the theory and assumptions (and their alternatives) underlying the structure of each model.

Key Words: community stability, ecological sites, ecosystem health, indicators, New Mexico, vegetation dynamics

Resumen

Los modelos del tipo de estado y transición han recibido mucha atención desde su introducción en 1989. Sin embargo hasta hace poco tiempo se cuento con diferentes modelos de 'estado y transición' que pueden ser usados por agencias gubernamentales y particulares. Existen pocos lineamientos disponibles para su desarrollo e interpretación. Basados en nuestra experiencia en el desarrrollo de estos modelos para el estado de Nuevo México, hacemos las siguentes preguntas: 1) ¿ como debe ensamblarse la información para crear modelos para sitios específicos en grandes regiones? 2) ¿ cuales aspectos ecológicos deben ser considerados en el desarollo del modelo y su clasificación? y 3) ¿ como deben usarse estos modelos ? Revisamos la estructura general de los modelos de 'estado y transición' enfatizando los cambios entre comunidades vegetales dentro de estados que son reversibles con los cambios en el clima y practicas facilitadoras (i.e. manejo de pastizales). Asi como cambios entre estados (transiciones) que son reversibles solamente mediante practicas aceleradoras como la resiembra, control de arbustos, y recuperación de la estabilidad y función hidrológica del suelo. las regiones climáticamente definidas (unidades de recursos terrestres) y los sitios ecológicos dentro de ellos sirven como estructura para el desarollo y selección de los modelos. También, ilustramos la importancia de delinear claramente los sitios ecológicos para producir los modelos y describir como hemos resuelto el problema de los sitios pobremente delineados. Para producir modelos específicos se requiere la comprensión de los mecanismos ecologicos que determinan las transiciones. Adicionalmente, mostramos como los modelos pueden representar y distinguir hipotesis alter-

We thank several agencies, institutions and individuals who contributed data, knowledge, and criticisms that are represented in this manuscript. From the BLM, Phil Smith, Lane Hauser, Rusty Stovall, Mike Ramirez, Susan Britt, and John Spain; from the NRCS, David Trujillo, Gene Adkins, Garth Grizzle, Darrel Reasner, Tim Henry, Frank Corn, Bill Schwebke, Arlene Tugel, and Pat Shaver; from the U. S. Forest Service, Wayne Robbie and Ralph Pope, from USDA-ARS, Bob Gibbens, from New Mexico State University, Gary Donart and Barbara Nolen; and private citizens, Jim Powell and Lee Gile. Alfonso Serna-Perez and Isaac Reyes-Vera translated the abstract. We thank Sam Fuhlendorf, George Peacock, Nathan Sayre, Mark Westoby, 2 anonymous reviewers, and especially Mitch McClaran for many valuable suggestions. That should not imply that these individuals agree with all that we have written, however.

Manuscript accepted 21 May 02.

nativas y/o complementarias para explicar las transiciones. Aun cuando puede haber varios mecanismos para explicar transiciones, estos se consideran dentro de categorias discretas basadas en unos pocos procesos ecologicos fundamentales y sus relaciones pueden ser facilmente comprendidas. El conocimiento de los mecanismos esta estrechamente ligado al uso de indicadores ecológicos para anticipar las transiciones. Concluimos que los modelos deben de incluir 1) valores de referencia para indicadores cuantitativos, 2) lista de indicadores clave y descripción de sus cambios que sugieran una aproximación a una transición, y 3) una documentación rigurosa de las teorias y asunciones (y sus alternativas) que dan base a la estructura de cada modelo.

Ecological theory provides a basis for land management. An understanding of the processes inferred to cause population or community patterns determines how managers should respond to patterns. A prime example is the succession-retrogression (or range condition) model of Dyksterhuis (1949) that is based on the successional theory of Clements (1916) and the edaphic polyclimax concept of Tansley (1935). This model emphasized the return of disturbed communities to a competitively-determined climax state and has been a guiding principle in range management (Westoby 1980). Upon recognizing an undesirable trend in plant community composition, managers could respond by reducing or redistributing grazing pressure and effect a return to desirable conditions. An important reason for the success of this model is that it provided a method to measure and compare land condition against the expectations of the model (i.e., the similarity index), thus providing a concrete link between theoretical expectations and management response.

Rangeland managers have long recognized that semiarid grasslands can transform into shrub-dominated states that cannot be returned to grassland through grazing management (Laycock 1991), contrary to applications of the succession-retrogression model. Assuming that a single, competition-defined equilibrium plant community should exist for each site, alternative states, and the rangelands in which they occur, have been referred to as "non-equilibrial" (following Wiens 1984). In fact, these alternative states may be highly equilibrial (e.g., Muller 1940) after the transition, so these systems are better termed multi-equilibrial. The increasing emphasis on processes other than competition in determining community patterns (Kingsland 1985), paved the way for Westoby et al. (1989, Westoby 1980) to propose a revised framework for range management. The state-and-transition model formally acknowledged the multi-equilibrial nature of many rangeland ecosystems and the rapid and unanticipated shifts among these equilibria. Furthermore, Westoby et al. (1989) focused attention on the multiple mechanisms underlying alternative equilibria and emphasized an "opportunistic" style of management in which strategies vary depending upon which mechanisms are important. The state-and-transition concept provides a means for anticipating departures from the monoclimax model and incorporating this understanding into management plans. Consequently, this concept is being widely espoused within the range science community of the United States (Society for Range Management 1995, USDA NRCS 1997). For agencies such as the Natural Resources Conservation Service (NRCS) and Bureau of Land Management (BLM), state-and-transition models promise to improve assessment, monitoring, and management in many semiarid rangelands.

Twelve years after the seminal publication of the state-and-transition concept, however, few applications of the concept exist that can be used by land managers. This is not to say that there has not been a great deal of work on the concept. Researchers have provided refinements to underlying ideas (Laycock 1991, Freidel 1991, Rodriguez-Iglesias and Kothmann 1997, Reitkerk and van de Koppel 1997), technological advances in the production and quantification of models (Wiegand and Milton 1996, Allen-Diaz and Bartolome 1998, Plant et al. 1999), and some site-specific conceptual models (e.g., Archer et al. 1988, Ash et al. 1994, George et al. 1992). There have been few attempts, however, to develop sets of site-specific models based upon existing information that can be applied by land managers in a systematic way over broad areas. Here, we relay some of the insights gained during the production of state-and-transition models for rangelands in the state of New Mexico, USA.

Like other western states, New Mexico is dominated by semiarid rangelands and the limitations of the monoclimax model are very apparent in many of these ecosystems. State-and-transition models have the potential to provide a framework for organizing complex sets of ideas about the multiple, interactive processes driving ecosystem change and the roles that management can play in directing these processes. The details of these models can draw upon a wealth of recent conceptual and technological advances in community and landscape ecology, including the relationships between positive feedback mechanisms and threshold changes in processes such as erosion (Davenport et al. 1998), the dependency of threshold changes on processes operating on different scales of space and time (Scheffer et al. 2001), and understanding the linkages among processes using ground-based and remotely-sensed patterns (Rango et al. in press). Implementing these advances to improve on-site management of rangelands, however, presents substantial challenges, among them: 1) how do we draw together the detailed information required to create site-specific models that are applicable across entire regions, 2) what ecological issues need to be considered in developing and classifying sets of models, and 3) given the models that can be produced, what do we want to use them for and how should they be used? In addressing these general questions about state-and-transition model development, we draw on examples from state-and-transitions models developed in a range of landscapes in New Mexico.

What is a state-and-transition model?

The idea that rangeland vegetation exhibits multiple states, and transitions among them, has been referred to generally as the state-and-transition model. These concepts have been adequately reviewed elsewhere (Laycock 1991, Brown 1994, Rodriguez-Iglesias and Kothmann 1997, Stringham et al. 2001). To be operational, however, specific state-and-transition models must be created that describe the details of vegetation dynamics for particular land areas. The graphical and conceptual format provided by Westoby et al. (1989), with modifications most recently summarized by Stringham et al. (2001; Fig. 1), illustrate several key elements that are communicated in these conceptual models. The model format presented here is based upon that currently used and presented by the NRCS.

As in vegetation mapping (Grossman et al. 1998), the most basic unit is the plant *community*. This is the relatively homogeneous assemblage of plants that occurs at a particular point in space and time, and can be defined at a scale relevant to a land manager (e.g., 0.1-10 ha). In the models for New Mexico, plant communities are

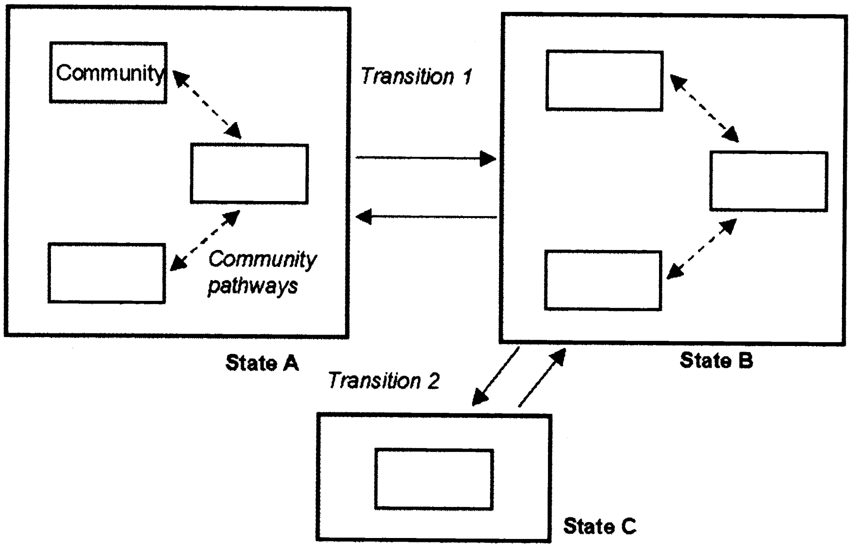

Fig. 1. The general structure of state-and-transition models after Stringham et al. (2001). The small boxes represent individual plant communities and the dashed arrows between them represent community pathways along which shifts among communities occur. These shifts are reversible through facilitating practices and fluctuations in climate. The large boxes containing communities are states that are distinguished by differences in structure and the rates of ecological processes (such as erosion). The transitions among states (solid arrows) are reversible only through accelerating practices (e.g. seeding, shrub control, or addition of soil) that can be applied at relatively great financial expense.

often defined by dominant species, or species that indicate the operation of particular processes (e.g., an encroaching shrub species, whether or not it is now dominant). Descriptions of plant communities may also contain information on soil conditions that indicate processes (e.g., the cover of physical, chemical or cryptogamic crusts). It is important to identify the range of plant communities in a land area because these are the observable and measurable links to the processes embodied in the remaining components of the model. Plant community identity at a location may vary in time and the arrows between communities indicate changes (or "community pathways") among them. These shifts in plant composition, as opposed to those referred to as "transitions" (see below), may be caused by climate or land use but are reversible by simply altering the intensity or direction of the factors that caused the change in composition (e.g., practices that reduce grazing pressure or increases in rainfall after a drought). The "facilitating practices" as defined by the NRCS (USDA NRCS 1997) would produce responses along community pathways. Thus, the succession-retrogression model operates along community pathways and is embedded within the state-and-transition model.

Communities are aggregated into states (Fig. 1) that are distinguished from other states by relatively large differences in plant functional groups and ecosystem processes and, consequently, in vegetation structure, biodiversity, and management requirements. For example, a grassland, whether it is dominated by one grass species or another, may provide sufficient cover to prevent rain-drop compaction of the soil surface and to intercept water and nutrients before they are lost from the system. In doing so, dominance by either grass species can sustain the soil conditions required by the other, and replacements along community pathways may occur within the state. Once grass cover has been reduced below a critical amount (Davenport et al. 1998), or a shrub species invades that leads to grass loss (Brown and Archer 1999), infiltration is reduced and erosion accelerates, a change in soil conditions occurs, and the system crosses into a new state. This new state is characterized by a distinct set of plant communities and a distinct range of values for ecosystem attributes.

The shift between states is referred to as a "transition". Unlike community pathways, transitions are not reversible by simply altering the intensity or direction of the factors that produced the change (c.f. the "amplitude" of Westman 1978) and instead require the application of distinct factors such as the addition of seeds, the removal of shrubs, or the addition of topsoil. These "accelerating practices" as defined by the NRCS (USDA NRCS 1997) are often expensive to apply. Generally, transitions among ecosystem states are thought to be caused by a combination of external and internal, positive feedback mechanisms that alter constraints on the presence or abundance of particular plant species (e.g., Schlesinger et al. 1990; Fig. 2). Three general classes of constraints can be recognized: 1) the dispersal of propagules to a site and subsequent reproduction, 2) "neighbor" constraints, including the effects of competitors, predators, or parasites, as well as the tendency of certain life-forms to facilitate fire disturbance, and 3) "site" constraints, including soil properties, hydrology, and climate. Transitions occur when 1 or more constraints are altered by external factors and this change catalyzes changes in positive feedbacks that produce relatively important shifts in vegetation structure and soil properties. Multiple external factors can be affected by singular processes, such as livestock grazing (e.g., by introducing shrub propagules and decreasing competition with them). Furthermore, changes in one class of constraints may reinforce changes in other constraints, such that several positive feedback mechanisms operate together (c.f. Archer 1989).

For example, heavy, continuous livestock grazing may initiate changes to shrub colonization ability by providing a dispersal pathway for seeds and reducing competition and fire disturbance by removing grasses. Reduced competition and fire disturbance may permit shrub establishment and growth. The presence of adult shrubs 1) increases shrub seed availability through reproduction and facilitates the dispersal of additional seeds to the site by attracting birds, 2) increases competition with grasses and limits grass reestablishment, and 3) increases erosion rates and nutrient loss from shrub-interspaces by reducing grass basal cover. Alternatively, prolonged and severe drought or mechanical disturbance (e.g., off-road vehicles) might catalyze a similar sequence of events if shrub seeds were already present.

Thus, different states can be viewed as separating positive feedbacks between different kinds of plants and different ecosystem processes. For example, by retaining soil nutrients and high infiltration capacity over relatively homogeneous areas (Ludwig et al. 1994), or by promoting fire (McPherson 1995), grasslands sustain themselves. By promoting intershrub erosion and heterogeneous nutrient distributions, or by outcompeting grasses for water, shrublands promote shrublands (Schlesinger et al. 1990). Once competi-

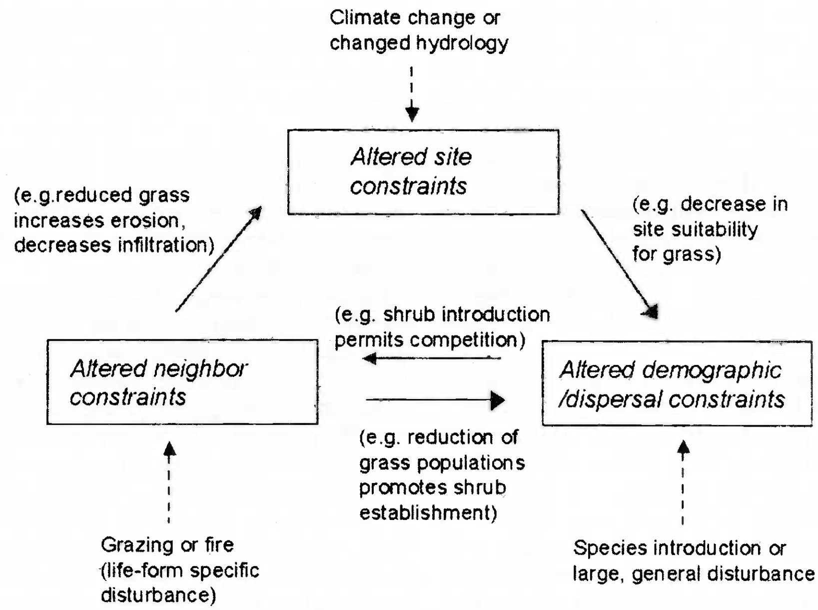

Fig. 2. The relationships among the classes of constraints that are altered to produce an ecosystem transition, and the internal and external processes that affect these constraints. External processes (dashed arrows) act as environmental triggers that set in motion positive feedbacks represented by the internal processes (solid arrows). Processes affecting particular constraints interact with one another such that multiple mechanisms produce and maintain transitions. See text.

tive dominants are introduced, species are lost, or soil properties are significantly altered, transitions can be difficult and expensive to reverse. An understanding of the constraints to ecosystem change, and the relationships between the external and internal mechanisms affecting them, suggest strategies for predicting and avoiding transitions and devising restoration strategies (Whisenant 1999). Although the causes of individual transitions in models are varied, the mechanisms involved fall into readily-understood classes (Fig. 2) that are common to all models.

State-and-transition models, then, represent postulates about the causes of both ephemeral and persistent changes in vegetation at a site and should offer testable predictions. Moreover, the models provide a logical framework in which assumptions and concepts about how rangelands work must be specified. This can add clarity to our ideas about rangelands, and often reveals how little we really know about them.

Model classification using ecological sites

Before a model can be created and tested, it is critical to define the extent over which a single model will apply. For arid rangelands in the United States, this extent is currently defined by the *ecological sites* of the NRCS (USDA NRCS 1997). Historically, ecological sites (previously called *range sites*) were based solely on similarities in the composition and productivity of dominant, climax vegetation (Shiflet 1975). Ideally, ecological sites are a classification of land types based on differences in important environmental factors, including soil properties, slope, and landscape position (e.g., in an upland or swale). These differences correspond to differences in the structure of plant communities, and with respect to state-and-transition models, plant community dynamics in the face of natural and human-caused disturbance (Society for Range Management 1995). Ecological sites are mapped by grouping soil mapping units on which plant communities are assumed to behave similarly. Ecological sites occur together in a landscape as a mosaic determined by patterns of geomorphology (Fig. 3c). Like other vegetation classification systems, ecological sites are nested within a hierarchy of climatically-defined regions (Fig 3a, 3b). The extent of a particular ecological site is bounded within an area of similar geology and climate, the *land resource unit* of the NRCS or *ecoregion* of the U.S. Forest Service, beyond which analogous ecological sites may exist. Thus, a particular state-and-transition model is intended to apply to one ecological site that can be found within only one land resource unit.

The definition of ecological sites (Creque et al. 1999) and land resource units is often arbitrary. Given the importance of soils and climate for the nature of vegetation dynamics, the validity of any state-and-transition model will depend upon the amount of variation in important

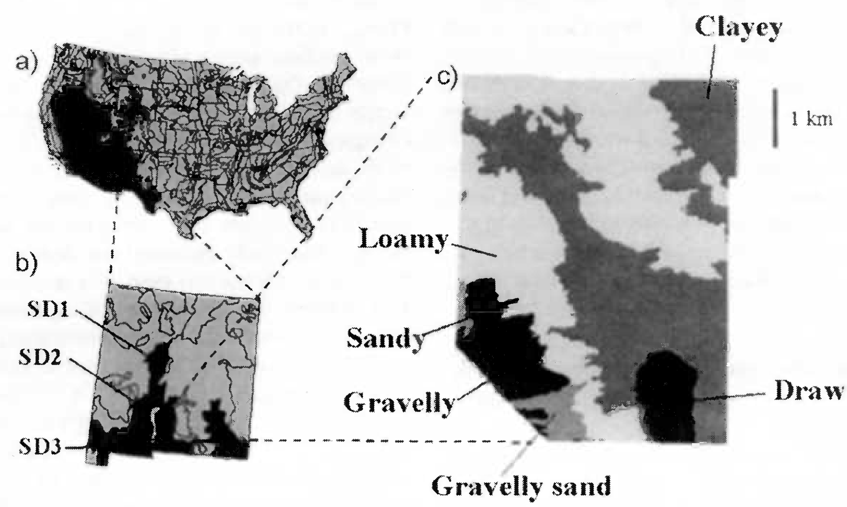

Fig. 3. The land-unit classification framework within which state-and-transition models are being developed by the Natural Resources Conservation Service. a) the Land Resource Region scale, highlighting the Western Range and Irrigated Region within which land resource units are embedded, b) the Major Land Resource Area scale: Southern Desertic Basins, Plains, and Mountains within New Mexico. Land resource units (SD-1, SD-2, SD-3) are noted with arrows. A unique set of ecological sites and state-and-transition models are common to each subresource area. c) a map of ecological sites for part of the Jornada Experimental Range based on groups of related soil series (draft soil map courtesy of Dr. Lee Gile and Barbara Nolen, the Desert Soils Project).

soil properties and climate within ecological sites and land resource units, respectively. If land assigned to ecological sites does not exhibit consistent properties, it may not be clear whether the variation in plant communities observed between 2 areas within the same ecological site is due to a vegetation transition or to static differences in environmental conditions (Friedel et al. 1993). For example, burrograss (*Scleropogon brevifolius* Phil.) is a mat-forming native perennial grass of the Chihuahuan Desert, is often dominant on loamy or clayey ecological sites, and is relatively unpalatable to livestock. Thus, dominance by burrograss is often assumed to be related to management practices and drought. While this may be the case on Stellar clay loam soils that were formerly dominated by tobosa (*Pleuraphis mutica* Buckl.), burrograss may have been historically dominant on Reagan clay loam soils (Leland Gile, personal communication). Reagan soils are highly calcareous at shallow depths relative to Stellar (see Gile and Grossman 1997) and are less pervious to water than are Stellar soils in a similar landscape position (Herbel and Gibbens 1989). Although Stellar, Reagan, and other soils have been grouped within the same ecological site, these soils clearly exhibit distinct properties and have probably always harbored distinct communities.

To distinguish management-produced from natural patterns (especially in the absence of historical data), it will be necessary to rigorously delineate ecological sites (Creque et al. 1999). Doing so will require that we distinguish ecological sites based upon values of soil and climatic variables that correspond to differences in the nature of state-and-transition models. In turn, this necessitates a detailed documentation of the relationships between plant communities and their dynamics to soil series. Such efforts will in many cases lead to reassignments of soils to ecological sites and the creation of new ecological sites.

Building state-and-transition models

Defining communities and community pathways

Once an ecological site has been selected, the first task in creating a state-and-transition model is to define the communities that can occur within that ecological site. A key benchmark is represented by the "historic climax plant community" of the NRCS (USDA NRCS 1997). This community represents the composition of plants that is known or is presumed to have dominated an ecological site prior to the settlement of Europeans, and is highlighted in the ecological site description. Furthermore, this community is often believed to be the one in which soil resources and native biodiversity is best conserved (but see Belsky 1996). Thus, the state bearing this community (along with related successional stages) is the global management standard of the BLM and the standard is implicit in the activities of other agencies and non-governmental organizations (c.f. USFS 2000, Bureau of Land Management 2001, Strittholt and Boerner 1995).

There are, however, several limitations to the historic climax plant community concept. First, in much of the western United States, the historic climax plant community does not now exist and cannot be reliably estimated from historical records. Thus, historic climax plant communities are sometimes estimated with the hidden assumption that the plants that were most palatable to livestock were the competitive dominants in the historic climax plant community (Westoby 1980). Second, the notion of the competitively-determined climax state is explicitly acknowledged in the historic climax plant community, and this is at odds with the multi-equilibrium concept now embraced by agencies (Svejcar and Brown 1991). That is, climaxes may shift, even without human influence, such that a climax is a "moving target" over broad time scales due to climate change (Brown et al. 1997). For example, it is possible that the dominance of black grama (*Bouteloua eriopoda* (Torr.) Torr.) on sandy soils of southern New Mexico was a consequence of climatic conditions peculiar to the late nineteenth century (Neilson 1986). A regional change in climate may now preclude sufficient sexual reproduction to reestablish black grama as a dominant in many areas, and it is possible that overgrazing and drought have only hastened the demise of this species. Given this case, it is questionable whether the restoration of a productive black grama-dominated community would be a suitable management goal. Third, aggregating soils with distinct inherent properties into ecological sites leads to the development of uniform expectations where they may not be warranted. For example, creosotebush (*Larrea tridentata* (DC) Cov.) has likely been dominant on erosional fan remnants at the base of Mount Summerford in southern New Mexico since before European settlement (Wondzell et al. 1996). The ecological site in which these soils are now grouped (Bulloch and Neher 1980), however, would lead one to the conclusion that creosotebush had encroached and displaced climax native grasses. Defining appropriate management standards via the state-and-transition (or the succession-retrogression) approach requires that we acknowledge and accept data limitations, take into account the multi-equilibrium nature of plant communities, and develop ecological sites based on a detailed understanding of plant-soil relationships.

Defining the range of alternative communities occurring in several ecological sites can be accomplished using monitoring data, such as those gathered by the Long-Term Ecological Research program, the BLM, the NRCS, private individuals, as well as repeated aerial or terrestrial photography from a variety of sources (e.g., Callaway and Davis 1993, Miller 1999, McClaran et al.). In many cases however, the number of ecological sites monitored or the duration of monitoring is limited. Interviews of rangeland professionals, researchers, and ranchers (Bellamy and Brown 1994) in conjunction with structured, rapid vegetation surveys based on soil maps and associated with soil series determinations can add significantly to the number of communities encountered and provide rigorous associations of communities with soil properties.

A practical limitation of using professional testimony and casual field observations to define communities is that it is often unclear how communities are related in time. The number of communities included within an ecological site may be an artifact of the persistent environmental heterogeneity in space included within an ecological site definition, rather than temporal variability at points in space. When it is suspected that 2 communities do not occur at the same points in space, the creation of a new ecological site may be called for. Alternatively, (or while new ecological sites are developed), we can denote the absence of temporal relationships among communities by having them "float" within the state and not be connected to other communities by community pathways (Fig. 4). In other cases, areas with differing aspect or slope are circumscribed in ecological site definitions, and northern and southern exposures may exhibit distinct species composition and dynamics. Nonetheless, these areas function similarly enough (or are so predictably associated) that they are considered within the same ecological site and state.

Defining states and transitions

States have been defined based on shifts in plant community structure using multi-

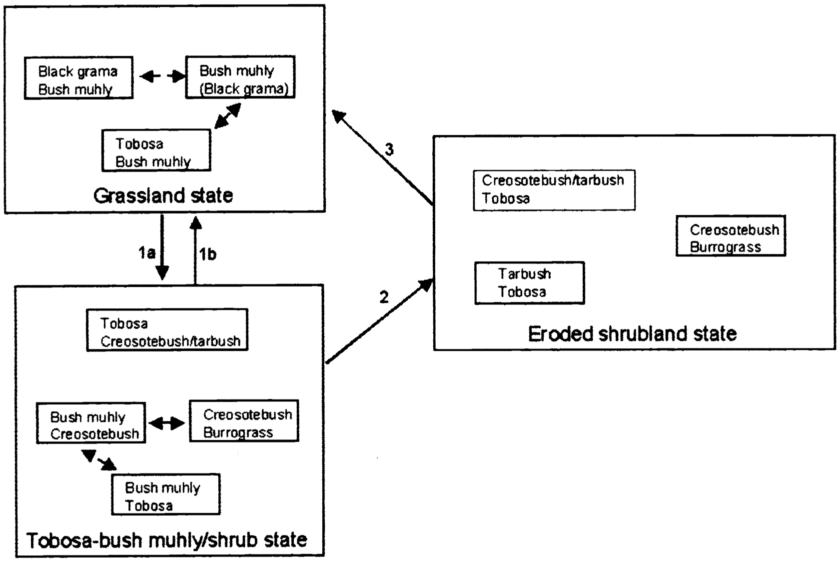

Fig. 4. A draft state-and-transition model for the gravelly loam ecological site within the SD-2 land resource unit of southern New Mexico. Transition 1 is caused by grass loss and subsequent shrub invasion, whereas transition 2 is caused by soil degradation. Transition 3 requires shrub removal, grass seeding, and restoration of soil fertility and permeability. The communities within the eroded shrubland state are not connected by arrows, indicating that there is no evidence for replacement among these community types. Instead, these distinct community types seem to reflect variation among soils included within the ecological site, although there is not yet enough information to reliably split soils into separate ecological sites. Black grama, bush muhly (*Muhlenbergia porteri* Scribn.), tobosa, and burrograss are perennial grasses; burrograss is usually least palatable to cattle. Creosotebush and tarbush (*Flourensia cernua* D.C.) are shrubs.

variate analyses of long-term data sets (Allen-Diaz and Bartolome 1998). While this approach is objective and potentially repeatable, it does not consider the processes or mechanisms involved in community changes. Furthermore, most applications do not demonstrate that plant communities have entered a new domain of variability (e.g., Friedel 1991) that indicates a fundamental change in the functioning of the ecosystem (Whisenant 1999). Thus, it is unclear whether changes in plant composition can be reversed through facilitating or accelerating practices (Stringham et al. 2001).

Given these uncertainties and the paucity of long-term data supporting the existence of multiple domains of variability, states and transitions can be constructed based upon postulates of vegetation change in combination with empirical observations of community structure and environmental conditions. For example, a number of explanations for the well-documented loss of black grama and increase in honey mesquite (*Prosopis glandulosa* Torr.) may pertain to Sandy ecological sites in south-central New Mexico (Fig. 5). The transition to a black grama-limited state (transition 1a) represents the shift between climatic or soil fertility conditions conducive to black grama dominance and conditions that lead to dominance by other species (Neilson 1986). Changed climate or further soil degradation may lead to black grama extinction and dominance by bunchgrasses that are able to reproduce by seed (transition 2). The transition to a shrub-invaded state is catalyzed by either the introduction of mesquite propagules into grassland (Brown and Archer 1987) or by the competitive release of existing mesquite seedlings through the reduction of grass cover (Van Auken and Bush 1997), fire frequency (Wright et al. 1976), or shrub seedling herbivores (Weltzin et al. 1997; transition 3a). Alternatively, propagule introduction might occur after or concurrent with a change in climate or soil degradation (Hennessy et al. 1983; transitions 4a, 5a). Initiated by these external triggers, the loss of black grama may be caused by a shift in positive feedbacks involving competition, erosion, and physical and chemical changes to soils (Schlesinger et al. 1990, Herrick et al. 2002) due to the presence of shrubs (transition 6). Shrubs would need to be removed to return to the black grama-dominated (transition 3b) or limited (4b) state. Shrub expansion may need to be controlled in order to remain in the shrub-invaded state, although coexistence

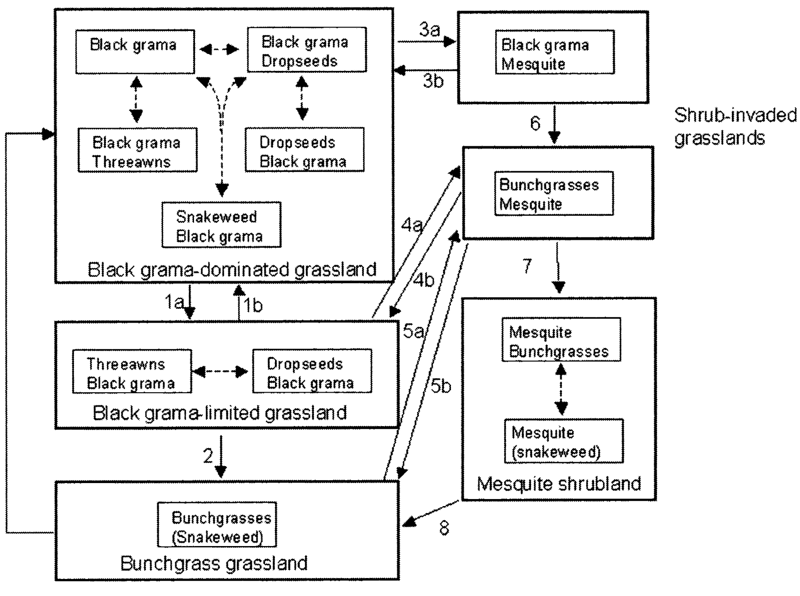

Fig. 5. A state-and-transition model for the sandy ecological site within the SD-2 land resource unit of southern New Mexico. Black grama, dropseeds (*Sporobolus* R. Br. spp.) threeawns (*Aristida* L. spp.) are perennial grasses. Black grama is palatable to cattle for a longer duration than the other species and comparatively sensitive to grazing pressure. Snakeweed (*Xanthocephalum* Willd. spp.) is a subshrub that tends to invade with reductions in grasses or with adequate winter-spring precipitation. Mesquite is a large shrub that tends to invade intact or degraded grasslands, promote the loss of grasses in intershrub spaces, and concentrate resources beneath its canopy.

between bunchgrasses and mesquite without shrub control may persist for long periods if soil degradation is not aggravated by environmental stress. If grazing, drought, or shrub encroachment continue to reduce the remaining grass cover, erosion and/or increases in rodent and rabbit densities (Campbell 1929) eventually lead to the formation of stable coppice dunes with the loss of most grasses (transition 7). At this point, natural reestablishment may not be possible for most grass species. In principle, the mechanical restoration and stabilization of topsoil and addition of soil nutrients and microorganisms following shrub removal could be used to initiate grassland recovery (transitions 8, 9)

In this example, the definition of each of the states depend critically on our notions of the processes driving vegetation change and our responses to them. For example, the shrub-invaded state may be defined by either the presence of shrub seedlings, or the presence of shrubs seedlings in the context of particular stresses or changes to disturbance regimes. If the presence of shrubs with grasses for long periods accelerates grass loss, a shrub-invaded state may be supported only by intensive accelerating practices. Alternatively, this situation might simply be considered as an early stage of a shrub-dominated state if shrub control was not implemented. In addition, we proposed that some communities (e.g. the dropseed/black grama community) occur in 2 distinct states. This denotes that communities with similar vegetation structure may have very different responses to management due to differences in climate or soil properties between the states. States are human constructs that represent our understanding of and relationships with rangelands.

By definition, the recognition of states and transitions also depends on temporal scale (Friedel 1997) and, thus, our ideas of stability and equilibrium. In many cases, such as when grasslands are converted to mesquite dunes, the difference between community pathways and transitions between states is clear. In other cases, it is not. For example, bottomland/draw system degradation in the New Mexico Plateaus and Mesas land resource unit may exhibit a cyclic sequence of "states" over a period of 50–100 years without the use of accelerating practices (G. Adkins, NRCS, personal communication). Erosion and channelization due to reduced grass cover leads to decreased soil moisture availability and a transition from giant sacaton (*Sporobolus wrightii* Munro) or alkali sacaton (*S. airoides* (Torr.) Torr.) grasslands to blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud. Hitchcock) grasslands characteristic of upland sites. Subsequently, agradation of soil into channels will lead to a return of flooding cycles, and bottomland grasslands may reestablish with improved grazing management. Ecological sites and regions may differ in the degree to which hydrology, climate, or other physical features create stability over particular time scales, blurring the distinction between pathways and transitions among "stable" states (Fuhlendorf et al. 2001). Nonetheless, when intensive accelerating practices (such as gully stabilization) can be used to hasten relatively slow natural processes or recovery, the recognition of distinct states is useful. Stability must be defined relative to a time scale, so it is important to consider how the scale over which natural recovery is observed matches management timeframes when defining states.

The relationship between states, transitions, and ecological sites

When a transition involves changes in soil structure, the resulting vegetation/soil change may be so permanent that it is considered a new ecological site rather than a state. The NRCS National Range and Pasture Handbook states "Severe physical deterioration can permanently alter the potential of an ecological site to support the original community" (USDA NRCS 1997). This may apply when soils are truncated to the point where an eroded phase is recognized in soil classification. For example, the loss of sandy surface horizons on some sandy loam soils may expose clay-rich strata that no longer support the germination or survival of formerly dominant species (Gile and Grossman 1997). The point at which a new ecological site should be recognized, however, depends on the fuzzy distinction between changes that are "persistent" (Stringham et al. 2001) without the use of accelerating practices (i.e., a transition) and "permanent" change. We should also be aware of the consequences of losing track of the occurrence of historic communities at a site—do we want to maintain documentation that a particular area used to be grassland but is now shrubland? The amount of financial resources required to apply accelerating practices to reverse a transition may be a suitable criterion for deciding when to create a new ecological site. Constraints due to biotic interactions, for example, are often less expensive to overcome than abiotic limitations (Whisenant 1999). We suggest, however, that the concept of "state" may be sufficient to describe persistent changes due to various causes and creating new ecological sites would be an unnecessary semantic complication.

Unexpected transitions among states (or sites) may depend upon the transitions occurring in adjacent sites. On the loamy soils of the Jornada Experimental Range, for example, wind erosion of degraded sandy soils to the west of loamy soils has resulted in the accumulation of sand on the loamy soils (C. Monger, personal communication). These patches support black grama grass that is absent on the unaltered soils. Herbel et al. (1972) speculate that the increased abundance of tobosa relative to black grama and other grasses on lower piedmont clayey sites is due to the increased water run-on from degraded gravelly sites occurring upslope. It is important to recognize that some transitions may have extrinsic causes that depend upon landscape context rather than local management.

Patterns in sets of state-and-transition models

Given the issues and approaches discussed in the preceding sections, what generalizations can be drawn from the models we have created? To date, we have produced about 60 draft or completed models spanning 4 land resource units in southwestern-southcentral New Mexico. These land resource units intergrade with one another, and differ in subtle ways based on moisture and temperature (Table 1). Some of the patterns that we have observed can be compared among land resource units using models from a set of common ecological site types representing a gradient of landscape position and soil properties. In general, we see that more states per ecological site were generated for thermic, aridic soils of SD-2 (i.e., the southern desert unit 2 land resource unit) than for the soils experiencing more ustic and/or mesic regimes in higher elevation or more northerly land resource units. This may be due to 1 or 2 non-exclusive causes: 1) more ecological sites within relatively warm and arid regions are subject to a variety of processes that lead to several states (e.g. erosion plus shrub invasion or expansion; Table 1) and 2) land-use professionals recognize more states in SD-2 because of the relatively extensive research conducted there. Another feature apparent in the groups of models is the wide range in the number of states. Some models (e.g. SD-1 Hills) have only one state, implying that the site is resilient with facilitating practices alone and that

Table 1. The number of states and key constraints defining the states for 7 common classes of ecological sites within 4 Land Resource Units (e.g., SD-2) in southern New Mexico. The Land Resource Units chosen differ in mean annual precipitation (MAP) and soil moisture regime (MR) and/or mean annual temperature (MAT) and soil temperature regime (TR) but all occur within south-central to southwestern New Mexico. The number of states and key constraints are based on published literature and interviews with rangeland professionals. These models may be viewed at the NRCS New Mexico website: http://www.nm.nrcs.usda.gov/techserv/fotg/Section2/esd.htm

	MLRA 42, SD-2* Latitude: 31° 19' - 34° 24' Longitude: 105° 50' - 109° 02' 8-10" MAP;15.5°C MAT MR: Aridic TR: Thermic		**MLRA 42, SD-1*** Latitude: 33° 27' - 35° 21' Longitude: 106° 25' - 107° 07' 8-11" MAP; 13.3°C MAT MR: Ustic-Aridic TR: Thermic-mesic		**MLRA 42, SD-4*** Latitude: 31° 40' - 32° 30' Longitude: 105° 39' - 105° 55' 12-14" MAP; 15°C MAT MR: Ustic-Aridic TR: Thermic		**MLRA 36, WP-3*** Latitude: 32° 22' - 34° 35' Longitude: 106° 58' - 109° 02' 12-16" MAP;13.3°C MAT MR: Ustic-Aridic TR: Mesic	
Ecological Site	**# of states**	**Key constraints**	**# of** states	**Key constraints**	**# of** states	**Key constraints**	**# of** states	**Key constraints**
Bottomland	5	Gullying Blocked run-on[1] Mesquite invasion[2]	3	Gullying Blocked run-on	2	Gullying Blocked run-on	3	Gullying Blocked run-on
Swale/Draw	5	Gullying Soil sealing Blocked run-on Mesquite invasion	2	Gullying Blocked run-on	NA	---	NA	---
Clayey/Clay upland	6	Soil sealing Blocked run-on Shrub invasion Erosion/soil loss	2	Soil sealing Erosion/soil loss	2	Blocked run on Soil sealing	2	Gullying
Loamy (Draw)	4	Soil fertility loss Shrub invasion Erosion/soil loss	4	Soil fertility loss Erosion/soil loss	3	Creosotebush invasion Erosion/soil loss	2	Soil fertility loss? Gullying
Sandy/Loamy sand	6	Soil fertility loss Mesquite invasion Soil-surface instability Erosion	2	Soil fertility loss? Sand sage expansion	2	Sand sage[3] expansion	3	Mesquite invasion
Gravelly	3	Creosotebush expansion[2] Erosion/soil loss	3	Soil fertility loss Creosotebush invasion	2	Creosotebush expansion	4	Erosion/soil loss Juniper[4] invasion
Hills	2	Erosion/soil loss	1?	---	NA	---	3	Juniper invasion
Mean number of states**	4.8		2.8		2.2		2.8	

* MLRA refers to the Major Land Resource Area (USDA NRCS 1997), a climatically-defined unit within which Land Resource Units are nested. Land Resource Unit designations include SD 1-4 (Southern Desert units 1, 2, and 4) and WP 3 (Western Plains and Mesas unit 3). See also Fig. 3.
** Swale/Draw and Hills Ecological Sites were excluded from the mean because they do not occur in all Land Resource Unit's (Hills) or are functionally different (Swale/Draw).
[1]Blocked run-on refers to the alteration of surface hydrology by features such as dams, ditches, or roads that inhibit natural water run-on patterns
[2]Invasion refers to the presence of a plant species that was not present in historic communities, whereas expansion refers to increased density of a plant relative to its density in historic communities.
[3]*Artemisia filifolia* Torr.
[4]*Juniperus monosperma* (Engelm.) Sarg.

the succession-retrogression model adequately describes its dynamics. At a continental level, this may be true of many rangeland communities that are resistant to soil degradation, not dependent on surface hydrologic inputs, or not subject to invasion by competitive species.

Can we generalize about the importance of particular processes in different ecological site types or land resource units? In some cases, we find that the same types of processes are invoked to explain transitions in similar ecological sites: lowland sites such as bottomlands, draws and clayey sites are subject to changes in surface hydrology and surface soil structure and chemistry with respect to infiltration. Changes among states in upland sites such as sandy, gravelly, and hills sites are often subject to erosion and loss of soil fertility. The importance of shrub or tree invasion, on the other hand, seems to depend on the ecological site/land resource unit combination in question, although in some land resource units (e.g. SD-2) it is more important than in others. Overall, we see that a subset of common processes in various combinations explain vegetation dynamics within different ecological sites. This allows us to make some generalizations, while requiring that these generalizations be carefully evaluated for each ecological site and land resource unit.

Using models: proximate variables, indicators, and predicting transitions

The primary use of state-and-transition models is to depict the circumstances surrounding past vegetation changes on ecological sites and to use this information to anticipate and interpret changes in the future. Beyond this general function, identifying the operation of processes underlying transitions will be key elements in using models to improve land management. In many cases this is difficult to do, however, because we often do not fully understand the causes of observed vegetation changes, particularly their interactions.

A conceptual approach to deal with this is to postulate that there is usually a dominant proximate variable or a characteristic pattern of correlation among several variables that regulates particular transitions on ecological sites. In the southwestern U.S., the duration and timing of available soil water may be a key variable involved in many kinds of transitions (Whitford et al. 1995, Devine et al. 1998, Breshears and Barnes 1999; Table 1) and also relates closely to nutrient availability (Stafford Smith and Morton 1990, Reynolds et al. 1999, Dodd et al. 2000). Transitions may be due to threshold (non-linear) changes in the availability of soil water over time due to shifts in runoff patterns (e.g., percolation thresholds; Davenport et al. 1998) or to threshold responses of species performance to gradual changes in the soil water (e.g., species-specific soil moisture limitations). Thus, nonlinear responses may be caused by both positive feedbacks that create threshold changes in variables as well as through species tolerance limits (e.g., Austin 1985).

To anticipate transitions, we need to know something about the changes in proximate variables underlying threshold responses in vegetation and soils. Despite a wealth of information, these issues have seldom been directly addressed in New Mexico, or elsewhere. For example, is the persistent reduction of black grama abundance due to a reduction in soil moisture availability, reductions in the abundance of mycorrhizal fungi, a change in rodent herbivory levels, some other unconsidered factor, or a combination of factors? If soil moisture changes are important for black grama germination, survival, or reproduction, then, across what values of moisture availability do threshold responses occur? Are threshold or continuous changes in these variables observed in nature and what are the causes of this variation? Are threshold responses of particular species determined by the same environmental variables in all instances? Addressing these questions for key grass and shrub species will greatly improve our capacity to provide flexible, predictive models of transitions with management utility that link retrospective data and observations with comparative studies and experiments.

But what is a manager to do with state-and-transition models while we gather and synthesize these critical data? Even when mechanisms are fully understood, proximate variables such as soil moisture or mycorrhizal populations are going to be difficult to monitor directly or may change only after a transition. A promising approach is to measure factors related to key proximate variables that indicate the operation of processes that can be altered to prevent (or facilitate) a transition (Herrick 2000, Ludwig et al. 2000, Kuehl et al. 2001). For example, the presence, expansion, and spatial arrangement of bare ground patches or shrubs, reduction in soil stability, or the formation of rills, litter dams, and terracettes indicate erosion that reduces soil fertility and microbial populations, water infiltration, and may eventually truncate entire soil horizons (Unpublished data, Herrick et al.). Thus, a trend towards a transition involving one or several interacting mechanisms may be revealed by indicators, even when the precise mechanisms (and critical values) are not well known.

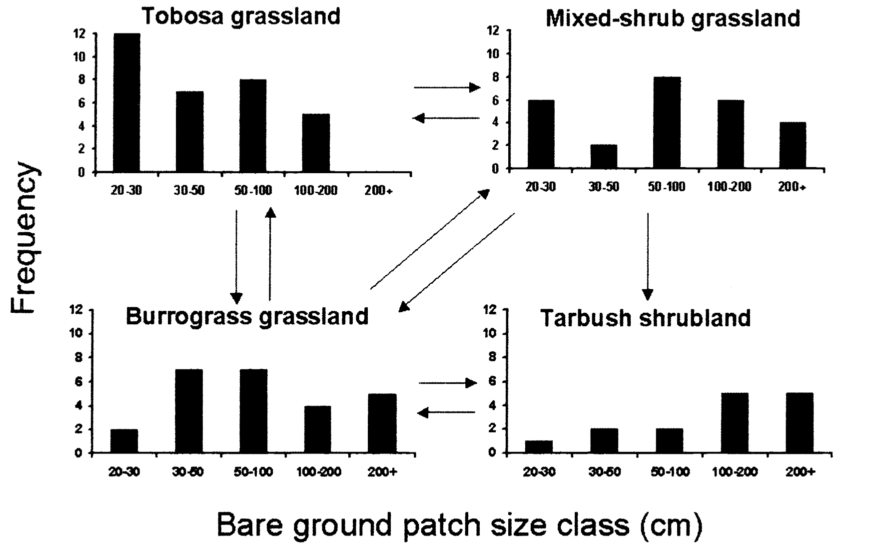

Fig. 6. Histograms for gap-intercept data (see Herrick et al. 2001) representing different states within the loamy ecological site in the SD-2 land resource unit of southern New Mexico. Graphs are arranged to parallel the state-and-transition model. Gap (bare-patch) sizes were measured along a 50-m tape. Gaps were the distance between perennial plant bases (where stems emerge from the ground) that were intercepted by the edge of the tape. Only gaps greater than 20 cm were tallied. Data were gathered on representative sites on the Jornada Experimental Range.

By linking specific indicators to state-and-transition models, model developers can provide tools to help land managers determine the state that land is in and to evaluate the probability of a transition. Different qualitative indicators (Pellant et al. 2000) relate to different processes, and models can point to specific indicators that signal an approach to a particular transition. Models can include ranges in values for quantitative indicators such as perennial plant cover, shrub density, bare ground patch size, frequency, and spatial arrangement, soil compaction, and soil surface stability to define the range of structure and function characterized by states and that provide benchmarks for measurements of the processes leading to transitions. In particular, indicators such as basal and canopy gap size (Unpublished data, Herrick et al.; see Fig. 6) are correlated with other indicators of soil quality and erosion and can easily complement the plant composition data gathered by management personnel to identify states. Together, the suite of qualitative and quantitative measurements can do for state-and-transition models what the similarity index does for succession-retrogression models: they provide a means to connect field observations with theoretical expectations and management responses.

It is important to recognize that transitions usually do not happen simultaneously across entire landscapes, grazing allotments, or even pastures. In many cases, transitions occur 1 patch at a time, occurring first on areas within ecological sites that are most sensitive to change due to slight variations in soils or landscape position (Fig. 7). Over time, or across space, these patches may coalesce to produce landscape-scale phenomena (Gosz 1993). Furthermore, changes in ecosystem functioning in 1 patch may affect adjacent patches. In many arid systems, nutrients lost from patches that have undergone transitions may be redistributed to adjacent patches, increasing local production and grass cover in those patches (Ludwig and Tongway 1995). These patch-scale dynamics indicate that 1) monitoring changes in the frequency, size, or spatial arrangement of patch-scale transitions may be used to indicate the consequences of management activities, 2) monitoring transects located in "nutrient sinks" or

Fig. 7. An area within the clayey ecological site on the Sevilleta National Wildlife Refuge north of Socorro, N.M. in the SD-1 land resource unit. Grasses in the foreground include galleta (*Pleuraphis jamesii* Torr.), alkali sacaton, and burrograss. This refuge has been excluded from livestock grazing since 1973. Despite rest, some large bare patches remain. These patches tend to have low soil aggregate stability indicating reduced capacity for infiltration. This suggests that a transition has occurred, albeit at a small scale.

insensitive locations will be incapable of providing early warning of a broad-scale transition, and 3) it is necessary to interpret fine-scale indicators within patches (e.g. Pellant et al. 2000) by considering patterns across entire landscapes.

Implications of state-and-transition models for management

As agencies and individuals adopt the state-and-transition model framework, and specific models are produced, it is important to consider how these concepts can change on-the-ground management and how the models will be used. First, the state-and-transition model implies that, for all practical purposes, some areas are incapable of being restored to a historic state by intensive accelerating practices. What constitutes "for all practical purposes" depends on the processes maintaining an undesirable state and the costs of reversing them. If a transition is determined by the lack of propagules of a dominant species at a site, it may be relatively inexpensive to reverse it. On the other hand, if the transition is caused by soil degradation, then the cost of reversing it would be far greater.

By assigning land to a state, we assert the existence of particular processes and constraints in that land that indicate management responses. For example, by assigning land within the gravelly ecological site to a creosotebush-invaded state, it is believed that the recovery of grass production may occur through use of a shrub-specific herbicide. In this case, competition for water and nutrients and propagule limitation define the properties of the state. On the other hand, if there had been a transition from the creosotebush-invaded state to the creosotebush-dominated state, the application of herbicide and seeding would be ineffective for regenerating a grassland state. State-and-transition models provide a framework for recognizing distinctions among the causes of vegetation change and distinguishing among these alternatives in the field.

The grassland-shrubland transition on gravelly soils also illustrates a potential hazard of the state-and-transition approach. Degradation-caused shrublands on gravelly soils may be presumed to be practically unrecoverable when they may, in fact, be recoverable through management practices (J. Powell, personal communication). If states are misidentified, sites may be "written off" prematurely, leading to missed opportunities and continued degradation. For this reason, local knowledge and open debate are necessary ingredients for applying state-and-transition models. State-and-transition models can convey what has happened on different soils, and what will happen given the operation of the processes embodied in a model. Managers can use case-specific information, supplemented with indicators in many instances, to evaluate the likelihood that particular processes are operating, evaluate management options with respect to those processes, and make a determination of the costs and benefits of those options. The refinement of transition-specific indicators and reporting of reference values with specific models will aid this process.

In using reference indicator values, it is ill-advised to consider maximizing grazing returns by pushing a rangeland as close as possible to a point of transition without "crossing" into another state. It is clear that temporally unpredictable and uncontrollable factors (e.g., climate) and a high degree of spatial variability in site properties (e.g., amounts of run-on, variation in soil gravel content) interact with factors under management control to cause rapid changes in key, proximate variables in space and time. Thus, it is doubtful that indicator values for specific transitions will be precise (Hobbs and Morton 1999, Muradian 2001). Management with respect to state-and-transition models calls for conservative strategies aimed at detecting and reversing trajectories toward variable environmental thresholds. This is the essence of "adaptive management" in the state-and-transition model context.

Conclusions and recommendations

State-and-transition models organize the combined understanding of scientists and managers to explain ecosystem dynamics across variable rangeland landscapes. It is important to recognize that this framework is not a blanket replacement of an outdated succession-retrogression model, but a complement to it that accounts for the existence of multiple equilibria, as well as the return to equilibrium following perturbations. Furthermore, the contrast between communities and states can be used to distinguish the need for facilitating and accelerating management practices. The results of a broad range of studies and personal experiences can be summarized within this framework and the resulting views can be continually updated as new observations and ideas emerge (Bradshaw and Borchers 2000).

In order for the understanding represented in state-and-transition models to be communicated, refined, and compared against the field observations of managers, we suggest the inclusion of several components in individual models. First, the catalog of states proposed by Westoby et al. (1989) can contain information that can be used to place land in ecosystem states and, consequently, provide benchmarks for assessing the risk of a transition. Ranges for quantitative indicator values, including line-intercept data of cover and species composition, belt transect data for invasive or encroaching species, gap intercept data (Fig. 6), and soil aggregate stability index values (Herrick et al. 2001) relate closely to many of the processes defining states in the New Mexico models that we have produced and form the core of the standard set of measurements we are currently gathering. The reference areas in which these data are gathered, (or estimates of reference values where such areas no longer exist) are selected by range professionals and scientists that contribute to model development. Second, the catalog of transitions can include a list of key qualitative and quantitative indicators, and descriptions of changes that occur in them, that suggest progress towards a transition. Finally, the hypotheses, assertions, literature and observations justifying the structure of each model should be documented. This allows the mechanistic foundations of models to be evaluated and challenged by the science and management communities so that model structures can evolve.

Collaborations between the management agencies and the research community will continue to play a large role in improving the utility of the state-and-transition model approach and several specific directions are indicated in this review. First, ecological sites and land resource unit delineations should be refined to better reflect key differences in soil, topographic, and climatic properties that create differences in vegetation dynamics. Multivariate analyses of broad-scale soils, vegetation, geomorphological (Gile and Grossman 1997, McAuliffe 1994), and climatic (Comrie and Glenn 1998) datasets can be extremely useful in the effort. Second, efforts must be continued to gather long-term data (in an experimental context where possible), stratified by soil series, and at appropriate spatial scales. Few experimental studies have directly addressed the constraints to plant dynamics on different soils (e.g., Northrup et al. 1999, Vandekerckhove et al. 2000), despite clear evidence that these constraints vary among sites. Studies of the mechanisms producing transitions are needed to interpret long-term vegetation data and develop suitable indicators. Third, both academic ecologists and resource managers should attempt to link information on other components of rangelands valued by land owners and society (e.g., biodiversity) to state-and-transition models so that their responses can be interpreted alongside those of plants and soils. (e.g., Van der Haegan et al. 2000, Bestelmeyer and Wiens 2001).

Our efforts in New Mexico lead us to conclude that a great deal of information has yet to be gathered, but that a great deal of understanding already exists that had not yet been captured in a useful form. The models we produced have been well-received by many field managers, for both complementing and organizing their knowledge as well as highlighting uncertainties. Models can improve the capacity of managers to evaluate the costs and consequences of management decisions and rally researchers around unanswered questions. For this reason alone, the production of state-and-transition models is a worthwhile endeavor. As models become firmly linked to a mechanistic understanding of plant pattern, dynamics and indicators of the processes underlying them, the models will become invaluable.

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J. Range Manage.
56: 127-132 March 2003

Hay-meadows production and weed dynamics as influenced by management

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Abstract

Managers of extensive livestock systems generally have 2 goals for permanent grassland management: to obtain sufficient dry matter to feed animals and to avoid the establishment and dominance of unpalatable species. Hay production in French Pyrenean meadows is dependant on the need to balance grazing and cutting dates to produce maximum biomass for hay stock and to prevent seed recruitment of *Chaerophyllum aureum* L., one of the major invasive unpalatable species. Experiments and observations on a set of meadows within farms show that optimal dates calculated from degree-days for cutting or spring grazing of *C. aureum* fitted to seed production and apex development respectively, decreases hay yield. This decrease is related to the earliness of the cut in regard to sward growth or to the biomass loss by senescence due to the vegetative regrowth of the sward after spring grazing. Compromises and choices have to be made for each meadow by the farmer according to its potential production, the risk of invasion by *C. aureum*, and its role in the forage system.

Key Words: management sequences, permanent grasslands, herbage growth, weed population demography

Resumen

Los manejadores de sistemas extensivos de ganado generalmente tienen dos metas para el manejo de zacatales perennes: Obtener suficiente materia seca para alimentar a los animales y evitar el establecimiento y dominancia de especies no gustadas por el ganado. La producción de heno en praderas "French Pyrenean" depende de la necesidad de balancear las fechas de apacentamiento y corte para producir la máxima biomasa de heno para almacenar y prevenir la acumulación de semilla de *Chaerophyllum aureum* L., una de las principales especies invasoras sin gustocidad. Experimentos y observaciones hechas en un grupo de praderas dentro de granjas muestran que las fechas optimas calculadas a partir de grados-día para corte o apacentamiento en primavera del *C. aureum* se ajustaron a la producción de semilla y desarrollo del ápice respectivamente y disminuyen el rendimiento de heno. Esta disminución es relacionada a lo temprano del corte con respecto al crecimiento de la pradera o a la perdida de biomasa por senescencia debida al rebrote vegetativo de la pradera después del apacentamiento en primavera. Arreglos y elecciones tienen que ser hechos por el granjero para cada pradera de acuerdo a su potencial de producción, el riesgo de invasión de *C. aureum* y su papel en el sistema forrajero.

In European livestock systems in mountain areas, grazed meadows often represent around 80% of the permanent grassland area at the farm level. The remaining 20% is grass used exclusively to yield hay or silage for animal wintering.

A critical point of this management system is to ensure, each year, sufficient dry matter yield of hay or silage to feed animals during the entire winter period (Theau et al. 1998). Any shortfall in stored feed requires hay purchases which threaten the economic sustainability of such systems. Topography and socio-economic trends favor valley bottom meadows, which are used both for grazing and hay production. Relatively recent changes in production organisation and in grassland management schedules (chronological order of farming operations and characteristics of the operations), have reinforced competition between grazing and cutting. Moreover, populations of undesirable species in permanent grasslands have markedly increased during the last few decades as a result of less intensive management practices in farming systems, leading to a reduction of grazing or cutting intensity (de Hullu et al. 1985, Bobbink and Willems 1993). Due to the unpalatable nature of these species, desirable forage species are often driven out by competition. For these reasons, total dry matter production and the proportion eaten by animals is reduced significantly.

Generally, the impact of management practices on biomass production and species population dynamics have been studied separately and very often only with regard to a simple technical operation (fertilization or grazing and cutting regimes). The purpose of this study was to define efficient grassland management systems that maximize dry matter yield and limit the population densities of undesirable species. Weed population control involves finding a better match between management patterns and sensitive phenological stages of the target species to maintain a constant or decreasing population growth rate. In this study, we used observations, surveys and experiments on a set of permanent meadows belonging to French Pyrenean livestock owners to assess the effect of cutting date, presence and date of spring grazing and manuring on dry matter yield at haymaking time and on the population density of *Chaerophyllum aureum* L. representing a major invasive perennial weed of meadows. We focused on the impact of these technical operations on recruitment of *C. aureum* seed as the most sensitive stage in the life cycle of this species (Magda and Jarry 2000).

Manuscript accepted 11 Jul. 02.

Materials and Methods

Study site: recording of management operations

Surveys of management regimes, herbage production and *C. aureum* population density were carried out on 52 meadows belonging to 4 farms in the Ercé valley in the Central French Pyrenees (0° 30' E, 42° 48' N). These permanent meadows are natural grassland communities with high species diversity. About 19 different species represent 90% of the grazed meadow biomass: about 60% of them are grasses (data not published).

These 19 or so species, along with higher altitude communally owned pasture, form the basis of traditional Pyrenean meat production systems. Each meadow management regime was identified from direct observations and surveys of farmers. The different technical operations (e.g., cutting, grazing, manuring, etc.) and their timing were recorded. Grazing takes place in spring and fall, before and after haymaking. Sward mean height after spring grazing was estimated from 50 sward stick measurements along a transect within each meadow (Duru and Ducrocq 1998). This height assesses the grazing intensity.

C. aureum life cycle, apex development and seed viability

Chaerophyllum aureum is one of about 300 species present naturally in permanent grasslands between 500 and 1,800 m in Europe (Gonnet 1989). Being very competitive, it is responsible for major infestations of hay meadows in less intensive livestock systems. Grazed only at a very early stage, it very soon becomes unpalatable to sheep and cows because of the concentration of lignified tissues in its shoots. It is a long-lived perennial (at least 7 years) that spreads solely by sexual reproduction, producing achenes which ripen from late July to late August and are distributed by dehiscence up to 20 m from the mother plant (Gonnet 1989). The seedbank is transient (Grime et al. 1988). Previous experimental studies on demography of *C. aureum* populations have elucidated its population dynamics strategy and identified sensitive stages in its life cycle in relation to management practices (Magda 1998, Magda and Jarry 2000). Restricting recruitment of new individuals is the only way to maintain or decrease population density by management of adult fecundity, seed dispersion and seedling survival.

The consequences of defoliation by grazing of the *C. aureum* adult apex on the development of reproductive structures were tested experimentally. The dynamics of apex development of *C. aureum* adults from spring regeneration were followed to determine the height of the apex within the sward at different times. Twenty-two plots (2.50 x 1.20 m) were located in an ungrazed meadow colonized by *C. aureum* with 8 replicate plots at each of the 4 observation dates. Ten main stems per plot were sampled every 12 days between the beginning of spring regrowth (23 March, i.e. at 394 degree days) and the end of vegetative growth (4 May, 782 degree days). The height above ground and length of each stem apex were measured at each date. After each sampling date, the 8 plots were cut to record the effect of removing the main stem apex on the reproductive capacity of the individual. Plots were cut with a mower, leaving a residual herbage height of 5 cm. This height was measured with a sward stick in most of the meadows after grazing.

Germination tests were done on *C. aureum* seeds after a period in manure to see whether manuring might affect long-distance seed dispersion for this species. Four cotton bags, each containing 100 seeds harvested from *C. aureum* populations established in the study site, were placed in January in 2 different manure heaps made the month before. Bags were placed at 2 different depths within each heap at 10 and 40 cm under the surface. Temperatures were recorded regularly with a Campbell thermocouple probe. Seeds were excavated the following spring (after 4 months) or a year later (after 16 months) to represent the times generally observed from farmers' practices between manure collection and its spreading. Seeds were buried in boxes filled with soil taken from the study site but from meadows not colonised by *Chaerophyllum aureum* and placed directly in the environmental conditions of the site. Seed germination rate was calculated from seedling surveys made in spring, which is the only time of year this species germinates. This rate was compared with that of control seeds which had never been stocked in manure but harvested at the same time and from the same populations.

Chaerophyllum aureum abundance surveys

Chaerophyllum aureum abundance was recorded within each meadow at 2 different dates in spring and summer on 4 x 0.25 m^2 plots. These 2 sampling dates were chosen to avoid underestimating populations as a result of missing juveniles in spring or intensively grazed adults.

Chosen at random over the whole meadow, the sample of 8 different plots allows the population to be estimated at the field level, taking into account thef spatial variation in density. Abundance was visually assessed for each plot, noting 1 if *C. aureum* was present, otherwise 0. Total scores for the whole meadow could thus vary from 0 to 8.

Correlations between management regime and abundance of *C. aureum* plants were analyzed by a non-parametric test adapted for small and independant samples, the so-called Wilcoxon-Mann-Whitney test (Scherrer 1984).

Herbage Mass Measurement

Each meadow's production was estimated by measurement of standing herbage mass from the same plots which were used to assess *C. aureum* abundance and taking into account the spatial variation of the sward over the whole meadow area. These measurements were made before spring grazing (20 April–19 May 1998) and summer cutting (4 June–13 July 1998) for the grazed meadows. For the ungrazed meadows, a first measurement of herbage mass was also made at the time of spring grazing. Each sward plot was cut at 2 cm above ground level with a small hand mower. Each plot biomass was weighed after drying at 80°C for 48 hours.

Nutrient indices determination

The herbage sampled for mass measurement was milled through a 0.8 mm screen and analyzed for nitrogen (Kjeldhal 1883), phosphorus (Murphy and Riley 1962) and potassium. To assess nitrogen status, we used the "dilution curve" method (Lemaire and Salette 1984). During herbage regrowth (after cutting or grazing), nitrogen concentration (N) decreases as the above-ground herbage mass (HM) increases according to the relation: $N\% = \alpha * HM^{-\beta}$, nitrogen being the nitrogen concentration in g per 100 g of biomass, herbage mass the above-ground herbage mass in tonnes of dry matter ha^{-1}, α the nitrogen concentration when herbage mass = 1 t ha^{-1}, β the coefficient of nitrogen dilution. With optimum nitrogen nutrition, the α and β parameters are constant for all species, even legumes: $\alpha = 4.8$ and $\beta = 0.32$ (Duru et al. 1997, Lemaire and Gastal 1997). We used the parameters of this control curve to calculate a nitrogen index (Ni) - the ratio between the measured nitrogen concentration of the above-ground herbage mass

(HM) and the optimum nitrogen concentration as previously defined (Lemaire and Gastal 1997):

$$Ni=100xN/4.8HM^{-0.32} \quad (1)$$

Critical herbage phosphorus and potassium concentrations were established, in relation with nitrogen concentration, and indices Pi (Phosphorus) and Ki (Potassium)were defined as the ratio between the actual phosphorus and potassium concentration and the optimal ones (Duru and Théllier 1997):

$$Pi=100xP\%/(0.15+0.065(N\%)) \quad (2)$$

$$Ki=100xK\%/(1.6+0.525(N\%)) \quad (3)$$

The indices could vary from 30 for very deficient herbage to 100 when the availability of nutrients allowed maximal growth.

Time scale definition

Two difficulties occur when comparing meadows for herbage mass production. First, meadows ranged from 600 to 1,000 m in altitude; secondly, biomass measurements were not made on all plots on the same date. For this reason, time is expressed in degree days (degree days) i.e. the accumulated daily mean temperatures from 1 February or from the previous defoliation. This date corresponds to a change in the response of leaf extension to temperature as a consequence of the transition from vegetative to reproductive development (Parsons and Robson 1980). A correction (–0.6°C per 100 m) was made to take into account the effect of altitude on temperature and so on growth processes.

Results

Management schedules

Spring grazing occurred on 32 of the 52 plots between about 500 and 1100 degree days after 1 February (Fig 1c), and the residual sward height varied from 3 to 18 cm (Fig 1d). Manure was spread on 40% of spring grazed meadows and on 82% of ungrazed meadows. The hay was cut after about 1500 degree days for ungrazed meadows and between 1200 and 1500 degree days for grazed meadows.

Herbage nutrient status and standing herbage mass

Herbage Ni varied from 55 to 85 (Fig. 1a). This means that on average, the nutrient supply from fertilizers and soil allowed the plants to reach 70% of their growth potential (Lemaire and Gastal 1997). The nutrients phosphorus (Fig. 1b) and potassium (not shown) indices were more variable, the lowest values being below 50 and the highest greater than 100. They were significantly mutually correlated (Test Wilcoxon-Mann-Whitney, $P<0.001$). Standing herbage mass at the hay stage varied from 1500 to 8000 kg/ha (Fig 1e).

At hay cutting time, the standing herbage mass (SHM) on ungrazed meadows averaged between 1000 and 1500 degree days (Fig 1e). It depended on the interaction between phosphorus and potassium nutrient status and time of harvest:

$$(SHM=-463 + \sum_{Feb1}^{HT}\theta[0.035Pi + 0.022\ Ki];$$

$$n=22,\ r^2 = 0.42,\ se = 742,\ P < 0.001) \quad (4)$$

There was no effect of nitrogen status on late hay yield but only one of phosphorus and potassium through stem growth (Duru and Calvière 1996). As there was a positive significant effect of accumulated temperature over the growth period, it means that for most of the plots, the maximum yield was not reached at the time where the herbage yield was measured, whereas the harvest period for 21 of the 22 plots occurred after 1100 degree days, which corresponds to the flowering period of most of the species (Calvière and Duru 1999). This result confirms experimental data for a range of nutrient supply treatments over 2 growing seasons (Calvière 1994) where it was observed that the dry matter accumulation increased up to 1500 degree days.

Following spring grazing, hay cutting time, averaged between 750 and 1000 degree days (Fig 1e). It was significantly lower ($P < 0.05$) than that of ungrazed meadows (54% on average) and positively correlated to the phosphorus status and the residual sward height (which reflects the intensity of spring grazing) and negatively correlated to spring grazing date:

$$SHM = 1931+32.6\ Pi +132\ RSH- \sum_{Feb1}^{GT}\theta\ (3.1);$$

$$n = 27,\ r^2 = 0.74,\ se = 400).$$

This means that the later the grazing time ($\sum\theta$) and the lower the residual sward height, the smaller was the standing herbage mass at the time of the hay cut. The difference in accumulated temperatures between spring grazing and hay yield times were not significant, meaning that the maximum yield was reached in the interval between the shortest (444 degree days) and the longest (956 degree days) regrowth times after grazing. This observation was in agreement with leaf lifespan for vegetative swards of cocksfoot (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea* L.), the senescence

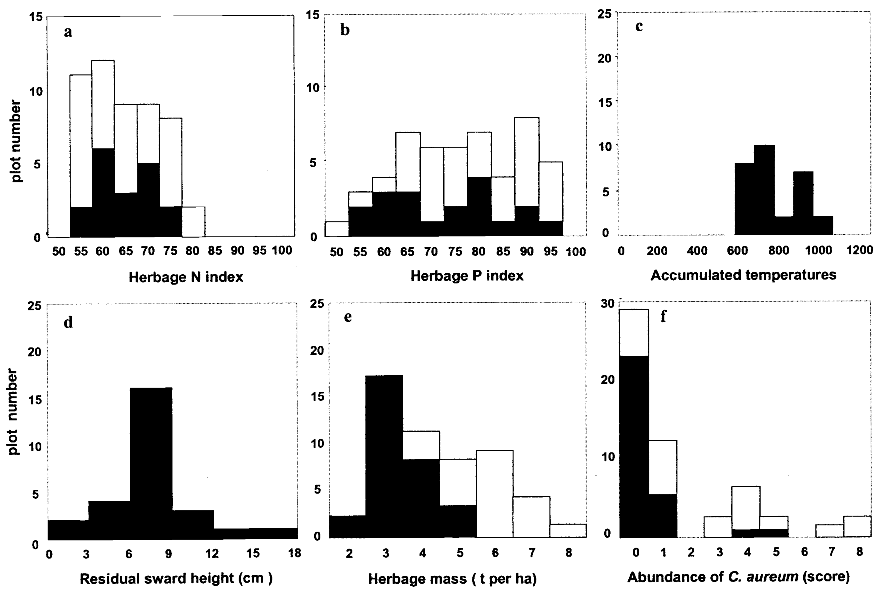

Fig. 1. Distribution of meadows (ungrazed in white; grazed in black) according to different variables. a) Herbage N Index, b) Herbage phosphorus index, c) Defoliation dates (degree days from 1 Feb.), d) Residual sward height after defoliation (cm), e) Herbage mass (kg/ah), f) Abundance classes of *C. aureum*.

process beginning at about 800 degree days (Duru et al. 1993), and the maximum yield being reached between 800 and 1000 degree days.

For both forms of spring management, maximum yield occurred when senescence rate became equal to growth rate (Parsons 1988, Scarnecchia 1988). When there is no spring grazing, it is reached at a high standing herbage mass and a later date because of the presence of stem material. Indeed, over the stem elongation period, photosynthesis rate increased up to 65% (Woledge 1978) and was related to the height of the apex (Leafe 1978, Parsons 1988). This increase in photosynthesis rate acts as a sink (Varlet-Grancher et al. 1982), but the proportion of stem depends on nutrient status (Duru et al. 2000) and on grazing management (Briske 1996). Intense grazing in the spring removes the apex of grasses and forbs, causing the plants to remain vegetative. Senescence rate depends on leaf lifespan and phenology of the species. Leaf lifespan, which determines the beginning of senescence, is relatively constant for a given species when expressed in degree-days (Duru et al. 1993). For vegetative swards, the senescence process involved the whole leaf, whereas over the reproductive phase, the stem component of the sward did not senesce, at least to begin with.

Spring grazing management had the greatest effect on standing herbage mass at the hay stage, and on the pattern of herbage mass accumulation. The effect of herbage nutrient status was less significant. We expected that, due to apex removal, standing herbage mass with spring grazing would be about 50% lower and would increase only up to 1000 degree days after grazing time, while it increased at least up to 1500 degree days after the end of winter when there is no spring grazing.

Impact of the technical operations schedule on *C. aureum* population density

Chaerophyllum aureum was observed throughout the range of nitrogen index (Ni) measured within the whole sampled meadows. However, it was less abundant at nitrogen indices < 56 (Fig 1a, 1f). Previous experimental studies have shown that a similar minimum fertility threshold (55 nitrogen index) is necessary for the establishment of *C. aureum* (Magda 1998). In this study site, the herbage nitrogen index varied from 55 to 85, indicating that all areas are liable to be invaded by this species (Fig. 1a). There was a significant and negative effect of grazing on *C. aureum* population density (Test Wilcoxon-Mann-Whitney, z = 5.6, P = 0.05), (Fig. 1f). About 56 % and 21 % of whole fields sampled fell within the abundance classes 0 and 1 respectively. Seventy six percent of the sampled fields which were not colonized by *C. aureum* were grazed. The 2 highest abundance values of *C. aureum* (abundance classes 7 and 8) were found only in ungrazed fields.

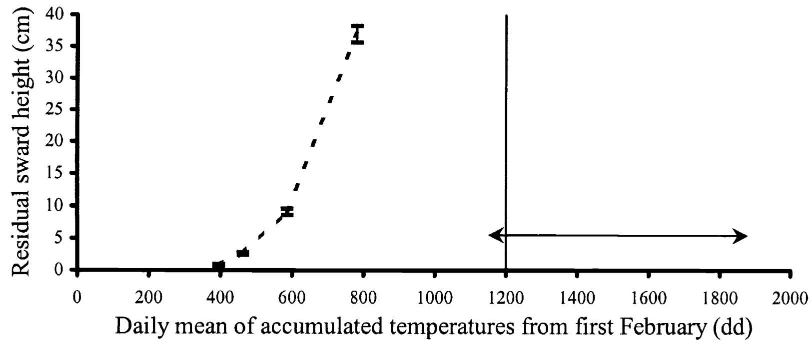

Fig. 2. *C. aureum* apex growth dynamics. Height of apex above ground (Y, cm) plotted against thermal time (X, Degree-Days) (dotted line) with a confidence interval calculated from a total of 280 measurements. The beginning of seed maturation period is represented by the vertical line. Horizontal line indicates the actual hay yield period.

These results clearly indicate the role of spring grazing in limiting *C. aureum* population density. Because adult resistance to defoliation has been already demonstrated (Magda 1998), these results confirm that grazing affects the recruitment process. It is likely that spring grazing first increases the seedling mortality rate due to trampling and biomass defoliation. We suspect that seedlings from emergence to the juvenile stage differ in sensitivity to biomass removal, but the most sensitive stage to grazing has not been determined. Secondly, spring grazing decreases the overall fecundity of the population by removing the shoot apex.

We show that apex removal during spring regrowth leads to purely vegetative stem development for *C. aureum*. To remove the main apex, date and height of defoliation through cutting or grazing has to be correlated (Fig. 2). This figure shows apex development schematically, so as to define the most efficient height for defoliation according to date of grazing or cutting. For example, for a spring grazing date at 600 degree days, the maximum threshold of residual herbage height was 11.8 cm. Moreover, at this date, *C. aureum* is not lignified and is entirely palatable for animals. Combining the data of Fig 1c, 1d and Fig 2, we deduce that for 24 of the 27 plots, the *C. aureum* apex must have been removed and that in most of the swards this species remained vegetative.

For the ungrazed fields, manure application was correlated significantly and positively to *C. aureum* population densities (Test Wilcoxon-Mann-Whitney, z = 2.26 P = 0.05). This confirms the hypothesis that seed can be imported with manure. Experiments on seed viability after storage in manure show that *C. aureum* seeds are capable of germination even after several months storage in manure and with greater success for seeds distributed near the heap surface when it is not turned over (Table 1). These results confirm the potential role of manuring in dispersing *C. aureum* seeds and in increasing the risk of seed immigration into fertilised meadows.

The fact that the effect of manure supply was not significant for grazed fields supports the view that grazing is a major factor limiting seedling establishment and/or population fecundity.

The presence of *C. aureum* in 13% of grazed fields can be explained by the spatial heterogeneity of grazing, which main-

Table 1. Percentage of germination on *C. aureum* seeds after a short or long period of storage in manure at 2 different depts, 10 cm and 40 cm under surface.

Control	Short stocking (4 months)		Long stocking (16 (months)	
	–10 cm	–40 cm	–10 cm	40 cm
	(%)			
69.6	72	0	61	0
	71	0	54	0

tains favorable microsites and consequently allows seedlings to escape from disturbance and mortality. Some adults of *C. aureum* could be also leniently grazed, particularly with late grazing. This phenomenon, in addition to heavy seed shedding, can maintain populations at a relatively high density within grazed fields. It can also correspond to transitory changes of management, creating an opportunity for *C. aureum* seedlings to be established.

To define the timing of the sensitive period for efficient defoliation for seed production control, phenological surveys have been conducted within *C. aureum* populations already established in hay meadows. Results show that cutting for hay before 1200 degree days prevents the seed maturation process.

Discussion

From results on herbage yield and *C. aureum* population demography, it is possible to propose a grazing and cutting schedule to optimize fodder production on hay meadows colonized by *C. aureum* (Table 2). For ungrazed meadows, 1 cut before 1200 degree days would prevent *C. aureum* seed production. Also, sward biomass losses associated with the development of reproductive structures would be limited because of the earliness of the cut.

Spring grazing could limit recruitment of new *C. aureum* individuals through 2 processes: enhancement of seedling mortality (Magda and Jarry 2000) and prevention of development of reproductive structures through apex removal for *C. aureum* and also for 3 grasses associated with *C. aureum* (not shown). Grazing efficiency is dependent on its intensity as defined by the residual herbage height, which determines the probability that the apex escapes grazing. The lower the grazing intensity, the greater is the likelihood that *C. aureum* adults will not be grazed. Nevertheless, the efficiency with which grazing removes the *C. aureum* apex will be related to the ingestion behavior of animals, grazing intensity (number of animals per unit of land area) and number of days of grazing. Moreover, as time passes and *C. aureum* plants mature, diet selection by animals will increase the probability for apex to escape to defoliation. Therefore, a lower limit of grazing date at 600 degree days is recommended, with a residual herbage height of 11.8 cm (Fig. 2). This date corresponds to the lower limit of apex height. Before this date, grazing does not remove the apex of many species and especially *C. aureum*. Delaying grazing, as well as increasing the grazing intensity, increases the probability of removing the stem apex for many grass species (Gillet 1980).

If the farmer wants to minimize any risk of seed production, hay cutting should occur before 1200 degree days. But in this case, hay yield is considerably depressed. Cutting should be done not later than 1000 degree days during the regrowth period to avoid losses through senescence. Finally, a choice has to be made by farmers: whether to ensure maximum yield production and accept a risk of recruitment of new individuals or to accept a compromise for hay production and ensure long term *C. aureum* population control.

In the case of hay meadows not already colonized by *C. aureum*, we believe that the risk of invasion is largely dependent on manure spreading. If no manure is applied, the risk of immigration of *C. aureum* seeds is relatively low and management can be based on maximizing hay yield. This risk is also low if the nutrient index is sufficiently low to prevent any natural colonization.

Manuring greatly increases the probability of seeds reaching non-invaded meadows, particularly when the meadows are not close to other seed sources. In this latter case, farmers can adopt a prevention strategy and maintain spring grazing to control potential seedling populations or take the risk and alter the management schedule only when adults appear in the meadow.

The demographic strategy of *C. aureum* populations is clearly characterized by a great ability to reach high densities and to maintain these densities for a long time. Prevention of establishment therefore appears to be the best management strategy for this species.

Conclusions

This study shows that the schedule of management operations to control weed species can be proposed from a knowledge of the developmental dynamics of the species and the demographic strategy of its population. Differentiation of population dynamics traits among grassland weed species is possible and allows different appropriate control strategies to be proposed. We have shown that spring grazing and cutting for hay can efficiently control *C. aureum* infestation when they are applied, relatively constantly, at appropriate dates for the morphological and reproductive patterns of this species. However, *C. aureum* population dynamics are not independent of forage species dynamics within the grassland community. The sequence of management operations

Table 2. Sequences and timing of technical operations (cutting and grazing) for control of *C. aureum* and maximazation of hay yield (degree days, standing herbage mass).

Sequence of technical operations	Limitation of *C. aureum* abundance		Maximization of hay yield
Hay cutting		<1200 degree days	<1500 degree days, standing herbage mass = f(herbage nutrient index)
Grazing - Cutting	Grazing	Cutting	• If grazing begins at < 600 degree days, the regrowth is reproductive → hay yield up to 1500 degree days should minimize herbage losses. • If grazing begins at >600 degree days, the regrowth is vegetative → yield time around 1000 degree days after beginning of grazing (about 1500 degree days after 01/02 if the swards were grazed at 600 degree days) should minimize herbage losses.
	<600 degree days	<1200 degree days	
	>600 degree days	<1200 degree days or not f(risk level accepted)	

needed to control *C. aureum* depresses herbage yield and could adversely affect forage production. Spring grazing limits the establishment of new individuals of this species but also reduces hay yield to that of the regrowth biomass.

In a given year, estimation of herbage losses, with or without spring grazing, has to be made according to the size of the *C. aureum* population and the corresponding herbage mass (mainly *C. aureum* stems) which was rejected when animals were fed indoors. Without control, *C. aureum* will always become rapidly dominant, suppressing the remaining species in the community. In this case, biomass is productive only if *C. aureum* is maintained at a leafy stage, preventing lignified stem development and this is possible only if defoliation occurs early in spring before stem apex development.

The conflict between forage production and weed control can be resolved at farm level. Limiting *C. aureum* recruitment and improving hay yields call for the revision of grazing and cutting operations, selecting productive areas for hay, reserving invaded areas for grazing, and generally preventing any seed immigration. Silage production could allow earlier cutting, i.e. before weed seeds mature. Reducing *C. aureum* seed viability by stamping manure could be another way of reducing the risk of seed propagation, especially on meadows on which there is a lot of biomass production.

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56: 133-139 March 2003

Moderate and light cattle grazing effects on Chihuahuan Desert rangelands

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Abstract

Vegetation changes were evaluated over a 13 year period (1988–2000) on moderately grazed and lightly grazed rangelands in the Chihuahuan Desert of south central New Mexico. During the study period, grazing use of primary forage species averaged 49 and 26% on moderately and lightly grazed rangelands, respectively. Autumn total grass and black grama (*Bouteloua eriopoda* Torr.) standing crop were consistently higher on the lightly than moderately grazed rangeland throughout the study. Total grass standing crop declined on the moderately grazed rangeland when the last 3 years of study were compared to the first 3 years (10 versus 124 kg ha^{-1}), but showed no change on the lightly grazed rangeland (320 versus 357 kg ha^{-1}). Black grama, the primary perennial grass in the Chihuahuan Desert, increased in autumn standing crop on the lightly grazed rangeland, but decreased on the moderately grazed rangeland. Dropseed (*Sporobolus* spp.) autumn standing crop decreased on both rangelands during the study. However, this decrease was greater on the moderately grazed rangeland (97% decline) than on the lightly grazed rangeland (67% decline). Perennial grass survival following a 3-year period of below average precipitation was higher on the lightly grazed (51%) than the moderately grazed rangeland (11%). Severe grazing intensities on the moderately grazed rangeland during the dry period (1994–1996) appear to explain differences in grass survival between these 2 rangelands. Our study and several others show that light to conservative grazing intensities involving about 25–35% use of key forage species can promote improvement in rangeland ecological condition in the Chihuahuan Desert, even when accompanied by drought.

Key words: Stocking rate, arid lands, livestock, range management

Resumen

Durante un periodo de 13 años (1988–2000) se evaluaron los cambios de vegetación en pastizales del Desierto Chihuahuense de la región sur central de New Mexico y que fueron apacentados ligeramente y moderadamente. Durante el periodo de estudio la utilización de las principales especies forrajeras promedio de 49 y 26% para los pastizales con apacentamiento moderado y ligero respectivamente. A través del estudio la biomasa total en pie de los zacates en otoño y la del "Black grama" (*Bouteloua eriopoda* Torr.) fueron consistentemente mayores en el pastizal apacentado ligeramente que en el apacentado moderadamente. Al comparar los últimos 3 años del estudio con los primeros 3 años se detectó que la biomasa total en pie disminuyo en el pastizal apacentado moderadamente (10 versus 124 kg ha^{-1}), pero no mostró cambios en el pastizal apacentado ligeramente (320 versus 357 kg ha^{-1}). El "Black grama", el principal zacate perenne del desierto Chihuahuense, aumento su biomasa en pie en otoño en el pastizal apacentado ligeramente, pero disminuyó en el pastizal apacentado moderadamente. Durante el estudio la biomasa en pie del "Dropseed" (*Sporobolus* spp.) producida en otoño disminuyó en ambos pastizales. Sin embargo, esta disminución fue mayor en el pastizal apacentado moderadamente (97% de disminución) que en el apacentado ligeramente (67% de disminución) La sobrevivencia de los zacates perennes después de un periodo de 3 años por debajo de la precipitación promedio fue mayor en el apacentamiento ligero (51%) que en el apacentamiento moderado (11%). Intensidades severas de apacentamiento ocurridas durante el periodo seco (1994-1996) en el pastizal apacentado moderadamente parecen explicar las diferencias en la sobrevivencia de los zacates entre estos dos pastizales. Nuestro estudio y algunos otros muestran que intensidades de apacentamiento de ligeras a conservadoras con un 25 - 35% de uso de las especies forrajeras clave pueden promover el mejoramiento de la condición ecológica del Desierto Chihuahuense, aun cuando se presenten sequías.

Chihuahuan Desert rangelands in the southern half of New Mexico and north central Mexico support nearly a half million animal units of livestock and numerous species of wildlife. Because of aridity and fragile soils, these rangelands are easily damaged by poorly controlled livestock grazing (Paulsen and Ares 1962, Buffington and Herbel 1965). Better information is needed on plant successional changes on Chihuahuan Desert rangelands under different stocking strategies. About 70% of the Chihuahuan Desert in southern New Mexico is controlled by the Bureau of Land Management (BLM). Generally, BLM rangelands are managed for multiple uses with a goal of about 50% use of perennial grasses over long time periods. In some years, grazing use may be lighter and other years heavier depending on annual precipitation. Various studies reviewed by Holechek et al. (1999) have indicated conservative grazing (about 35% use of

This research was supported by the New Mexico Agr. Exp. Sta., Las Cruces, N.M. 88003 and was part of project 0172944.
Manuscript accepted 8 Jun. 02.

perennial grasses) through time promotes increased forage productivity and may give higher financial returns than moderate grazing (about 45% use of perennial grasses).

During the 13-year period from 1988 to 2000, we evaluated long-term vegetation changes on 2 adjoining Chihuahuan Desert rangelands in southwestern New Mexico with similar soils, climate, and terrain (flat) that were assigned different stocking strategies. One rangeland unit was grazed lightly with the goal of 30% use of perennial grasses while the other was grazed moderately for 50% use. Variable stocking rates were applied to both rangelands taking into account changing forage conditions among years. Our objectives were to evaluate trend in forage production, herbaceous cover, brush cover, species composition, and rangeland condition on the 2 rangelands.

This research is a continuation of a long-term study initially reported by Holechek et al. (1994). During the 1982–1990 period, they found forage production increased on the 2 rangelands in our study in response to above average precipitation and conservative grazing use. Our study provides a detailed evaluation of vegetation changes on the 2 rangelands in the 1988–2000 period.

Fig. 1. The fenceline between the moderately grazed range (left) and lightly grazed range (right) in February 1991 (top) and February (2001) bottom.

Materials and Methods

Study Areas

Our 2 study areas were a lightly grazed site on the New Mexico State University Chihuahuan Desert Rangeland Research Center and an adjoining Bureau of Land Management (BLM) moderately grazed site (32° 32' 30" N 106° 52' 30" W) (Fig. 1). Both study areas are approximately 1,300 ha in size. The area is bound by the San Andres Mountains on the east and several isolated mountains on the west. Elevation varies from 1,190 to 1,380 m with level or gently rolling hills. Soils are primarily shallow, fine sandy loams (Aridisols) of the Simona-Cruces association (Tembo 1990). Topography is relatively flat with all slopes under 5%.

Long-term (1930–2000) average annual precipitation on the Chihuahuan Desert Rangeland Research Center is 23.6 cm yr^{-1}. Seasonal patterns of precipitation are characterized by small amounts in spring and a peak in late summer (August) with gradually reduced amounts during fall. A smaller peak occurs in early winter (January) (Pieper and Herbel 1982). Total and growing season precipitation were collected annually at 10 locations on the Chihuahuan Desert Rangeland Research Center rangeland (Table 1).

Vegetation is classified as Chihuahuan Desert grassland and shrubland (Paulsen and Ares 1962). Most of the grassland areas have been invaded by woody species during the last 100 years (Brown 1950, Dick-Peddie 1966). The principal vegetation communities are black grama (*Bouleoua eriopoda* Torr.) grassland, honey mesquite (*Prosopis glandulosa* Torr.) shrubland, creosotebush (*Larrea tridentata* Lar.) shrubland, and tarbush (*Flourensia cernua* D.C.) shrubland (Paulsen and Ares 1962, Pieper and Herbel 1982). Annual forbs include leatherleaf croton (*Croton pottsii* Lam.), nightshades (*Solanum* spp.), globemallows (*Sphaeralcea* spp.), and Russian thistle (*Salsola iberica* L.). The presence of these forbs is dependent on seasonal precipitation.

A detailed grazing history of the Chihuahuan Desert Rangeland Research Center and BLM study areas is provided by Holechek et al. (1994). Both areas were predominantly black grama grassland with a minor woody component when the Chihuahuan Desert Rangeland Research Center was established in 1927. Zones of degradation were minimized because watering points were widely spaced. Although information is vague, stocking rates on the Chihuahuan Desert Rangeland

Table 1. Total and growing season (July, August, September) precipitation (cm) on the Chihuahuan Desert Rangeland Research Center from 1988–2000.

	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	13 Year Average	Long-term Average (1930-2000)
	(cm)														
Total precipitation	30.0	19.3	21.2	38.4	39.1	25.1	17.8	17.0	20.1	29.5	20.8	28.0	27.4	25.6	23.6
Growing season (July, August, September) Precipitation	17.8	10.2	19.1	18.3	12.4	13.5	5.1	10.2	12.7	14.0	9.6	15.8	3.4	12.5	12.4

Research Center range averaged 40 ha per animal unit (AU), forage production averaged near 360 kg ha^{-1}, and forage use averaged about 35% during the 1930's and 1940's. On the adjacent BLM study site, stocking rates averaged 24 ha AU^{-1} and grazing use averaged between 60–70%. A continuous (year-long) grazing system has been used on both study areas from the past to the present. Black grama cover was greatly reduced on both study areas during extended drought in the 1953–1956 period. Herbicide treatments to control brush were applied to approximately 90% of the Chihuahuan Desert Rangeland Research Center study site in the 1957 to 1964 period (Holechek et al. 1994). Mesquite kill varied from 64 to 93%. The BLM study area received herbicide treatment in 1955, but no evaluations were made of percent mesquite kill or herbage response.

Grazing on the Chihuahuan Desert Rangeland Research Center study area has been carefully controlled since 1967 when the stocking rate was initially reduced to 67 ha AU^{-1} (Beck 1978, Holechek 1991, Holechek et al. 1994). During the 24-year period from 1967 to 1991, forage utilization averaged about 30%. Both rangeland ecological condition and forage production steadily increased. This allowed a gradual stocking rate increase from 67 to 45 ha AU^{-1} with no increase in forage use or sacrifice in cattle performance (Holechek 1992).

The general goal on the BLM rangeland since 1967 has been to remove about 50% of the perennial grass production. The stocking rate from the late 1960's to 1981 averaged 42 ha AU^{-1}. In the 1981 to 1990 period, the rancher destocked the range to an average rate of 72 ha AU^{-1}. This management change and above average precipitation resulted in a major increase in forage production and ecological condition (Holechek et al. 1994).

Procedures

Eight permanent transects (each 6.2 km in length) spaced 500-m apart were located across each study site (CDRRC and BLM) to evaluate vegetation canopy cover and standing crop. During the autumn of 1988, 1989, 1990, 1998, 1999, and 2000, incremental measurements of herbaceous foliar cover were taken seasonally along each transect using a modification (Holechek and Stephenson 1983) of the line intercept procedure outlined by Canfield (1941). At 100-m intervals, a 1-m rod incremented at 1-mm intervals was placed perpendicular to the transect and percent foliar cover was recorded by species. Each transect consisted of 64 sampling points. Three detailed measurements of shrub foliar cover were made at 2-km intervals along each transect using 40 x 2-m belt transects (Canfield 1941). These belt transects covered an area of 240-m^2 per transect.

Above ground standing crop (kg ha^{-1}) was sampled at the end of the summer growing season (October) from 1988 to 2000. Vegetation was clipped at ground level from 10 systematically located quadrats (0.5 x 1.0-m) placed at approximately 600-m intervals along each of the 6.2-km transects. Vegetation was hand separated by species in the field, oven dried at 60°C for 72 hours, and weighed. Only current-year's growth was measured. Livestock grazing was suspended on the BLM study area from 1 May 1998 to 1 November 1999 and during the growing season (1 July through 30 September) in 2000. This allowed us to evaluate herbage standing crop in the autumn on the BLM rangeland during the last 3 years of study without herbage removal by livestock during the growing season. Because the Chihuahuan Desert Rangeland Research Center rangeland was continuously (year-long) grazed, autumn current-year standing crop of forage underestimated ungrazed forage production. Forage use levels were light to conservative on both rangelands in the 1988–1990 period. Therefore, we consider autumn current-year growth to be a reasonable estimate of baseline herbage production. We made no adjustments for utilization.

Late June of each year was used to evaluate grazing intensity because it is the end of the forage cycle prior to new growth of perennial grasses which usually occurs in July (Paulsen and Ares 1962). Grazing intensity was evaluated on each study area using procedures of Anderson and Currier (1973) as modified by Holechek and Galt (2000). These procedures involved assessing grazing intensity on each study area through a combination of perennial grass stubble heights and ungrazed residual biomass of forage plants. Four permanent key areas were systematically established within each study area for these assessments. These key areas were selected by dividing each pasture into 4 equal parts and then locating the key area near the center of each part. All key areas were 1.3 to 1.8 km from water.

In October 1999, the percentages of live and dead perennial grasses were evaluated on all transects. The procedure involved recording the nearest plant at 200-m intervals along transects as live or dead based on the presence or absence of live above ground biomass. Dead plants were characterized by all blackish above ground biomass while presence of green or yellow above ground biomass characterized living plants.

Rangeland ecological condition scores were calculated from current USDA Natural Resources Conservation Service site guides for New Mexico (shallow sandy site) using the Dyksterhuis (1949) procedure. Relative percent composition of autumn current-year standing herbage on the Chihuahuan Desert Rangeland Research Center and BLM rangelands was used to calculate rangeland ecological condition scores for each year of study (1988–2000).

A repeated measures analysis of variance using the mixed model procedure of SAS (Littell et al. 1996) was used to compare autumn current-year total standing herbage, total grass standing herbage, black grama standing herbage and ecological scores across stocking strategies (2) and years (13). Transects were used as replications (8 per stocking strategy). Autumn herbaceous standing crop, standing crop relative composition, vegetation foliar cover, and foliar cover relative composition were compared on the lightly grazed and moderately grazed rangelands using data pooled across the first 3 years and the last 3 years of study. A randomized factorial analysis of variance was used with the 2 grazing treatments (light and moderate) and the 2 time periods (1988–1990, 1998–2000) as factors and transects (8 per stocking strategy) as replications. In an analysis of grazing experiments, Holechek et al. (1999) found data pooled across the first and last 3 years of study gave the most meaningful comparisons of long-term vegetation changes. This was because ecological condition and forage production were often not equivalent across grazing treatments at study initiation as in our case. The least significant difference mean separation procedure was used to compare means if analysis of variance indicated a significant ($P < 0.05$) difference (Steel and Torrie 1980). Comparisons of percentage of live plants between the Chihuahuan Desert Rangeland Research Center and BLM rangelands in 1999 were made using the standard t-test with the 8 transects in each treatment as replicates.

Results and Discussion

A comparative summary of stocking rate, forage utilization, vegetation standing crop, and rangeland ecological scores on the lightly and moderately grazed rangelands during the 13 year study period is given in Table 2. Stocking rate data in Table 2 are based on the forage cycle year starting 1 July (beginning of forage growth) rather than on the calendar year. This coordinates vegetation standing crop data collected in October with forage utilization data collected the following June.

Over the 13 year study period, total annual precipitation averaged 109% of the long-term average (23.6 cm yr^{-1}) (Table 1). During the first 6 years of study, annual precipitation averaged 122% of the long-term average. However, during the last 7 years, total annual precipitation was 97% of the long-term average. Drought occurred in 1994. Major stocking rate adjustments were made on both rangelands in response to changing precipitation and forage conditions (Table 2). The general approach on the lightly grazed rangeland was to stock at 70% of grazing capacity in years of above average to near average growing season precipitation and to destock under conditions of severe drought. Some minor adjustments were made in cattle numbers in the late autumn of each year. If at any time average stubble height of black grama dropped below 5.5 cm, the pasture would be completely destocked for at least 1 growing season. This occurred in late July 1994 and the pasture was immediately destocked. Restocking was not initiated until January 1997 because of poor forage growth in 1996 (Table 2).

On the moderately grazed rangeland, the approach was to stock at grazing capacity (230 animal unit years) unless excessive grazing (over 55% use of forage) was observed at the end of the forage cycle (June) for 2 consecutive years. If this condition was met, then the stocking rate would be reduced for at least 1 growing season. Recent precipitation conditions and forage availability in the pasture were also used in stocking rate decisions. If forage became severely depleted, complete destocking was an option. Major stocking rate reductions were made in 1994, 1995, 1998, 1999, and 2000 on the moderately grazed rangeland (Table 2).

Total vegetation, total grass, and black grama standing crop differed ($P < 0.05$) among stocking strategies and years (Table 2). Interactions between stocking strategies and years were significant (P <

Table 2. Stocking rate, forage use, forage production, and rangeland ecological condition scores for the lightly grazed and moderately grazed rangelands from 1988–2000.

	88/89	89/90	90/91	91/92	92/93	93/94	94/95	95/96	96/97	97/98	98/99	99/00	00/01
Lightly Grazed Rangeland													
Stocking rate (ha AUY^{-1})[1]	49	49	49	44	40	50	320	0	210	48	42	40	61
Forage utilization (%)[2]	33	28	33	22	18	33	50	0	10	33	38	18	31
Autumn vegetation standing crop (kg ha^{-1})[3]	527^{cd}	335^{e}	414^{d}	716^{b}	1006^{a}	281^{ef}	11^{h}	150^{g}	255^{f}	579^{c}	457^{d}	559^{c}	396^{de}
Autumn grass standing Crop (kg ha^{-1})[3]	452^{b}	270^{cd}	349^{c}	554^{b}	842^{a}	225^{d}	7^{e}	57^{e}	92^{e}	301^{cd}	305^{cd}	403^{bc}	252^{d}
Autumn black grama standing crop (kg ha^{-1})[3]	95^{ef}	68^{g}	59^{g}	119^{d}	380^{a}	86^{fg}	5^{i}	48^{h}	66^{g}	169^{cd}	120^{d}	222^{b}	115^{de}
Rangeland ecological condition score	62^{bc}	57^{c}	57^{c}	48^{cd}	59^{c}	53^{c}	56^{c}	64^{b}	81^{a}	72^{b}	68^{b}	88^{a}	74^{ab}
Moderately Grazed Rangeland													
Stocking rate (ha AUY^{-1})[1]	83	61	46	47	47	47	71	98	47	47	282	304	142
Forage utilization (%)[2]	21	31	38	33	30	48	60	75	80	75	85	20	45
Autumn vegetation standing crop (kg ha^{-1})[3]	229^{b}	227^{b}	420^{a}	405^{a}	500^{a}	210^{b}	45^{de}	22^{e}	78^{d}	160^{c}	134^{cd}	260^{b}	186^{bc}
Autumn grass standing crop (kg ha^{-1})[3]	104^{c}	108^{c}	159^{b}	201^{ab}	251^{b}	140^{bc}	13^{d}	3^{d}	18^{d}	12^{d}	2^{d}	8^{d}	20^{d}
Autumn black grama standing crop (kg ha^{-1})[3]	2^{c}	34^{ab}	2^{c}	38^{a}	49^{a}	20^{b}	$<1^{c}$	$<1^{c}$	3^{c}	$<1^{c}$	$<1^{c}$	$<1^{c}$	2^{c}
Rangeland ecological condition score	40^{ab}	48^{a}	31^{b}	34^{b}	39^{b}	40^{ab}	36^{b}	30^{bc}	26^{c}	22^{cd}	10^{e}	17^{de}	21^{cd}

[1]Stocking rate is for beginning of growing season (July 1) to end of dormancy the following year (June 30).
[2]Estimated in June of following year using procedures of Holechek and Galt (2000).
[3]Current-years growth unadjusted for grazing use.
a-iMeans within rows with different letters differ ($P < 0.05$).

Table 3. Average autumn herbaceous standing crop (kg ha^{-1}) and relative herbaceous composition (%) on lightly grazed (LG) and moderately grazed (MG) Chihuahuan Desert rangelands in south central New Mexico for the 1988–1990 and 1998–2000 periods.

Species or group	Autumn Standing Crop LG		Autumn Standing Crop MG		Standing Crop Relative Composition LG		Standing Crop Relative Composition MG	
	88–90	98–00	88–90	98–00	88–90	98–00	88–90	98–00
	(kg ha^{-1})				(%)			
Aristida spp.	60^{a}	45^{b}	13^{c}	2^{d}	14^{a}	10^{a}	4^{b}	1^{b}
Bouteloua eriopoda	74^{b}	152^{a}	13^{c}	1^{d}	17^{b}	32^{a}	4c	$<1^{d}$
Erioneuron pulchellum	4^{b}	t^{b}	21^{a}	3^{b}	1^{a}	$<1^{a}$	7^{a}	2^{b}
Muhlenbergia porteri	5^{a}	t^{a}	2^{a}	1	1^{a}	$<1^{a}$	1^{a}	$<1^{a}$
Sporobolus spp.	169^{a}	56^{b}	62^{b}	3c	40^{a}	12^{c}	21^{b}	2^{d}
Other grasses	44^{a}	66^{a}	13^{b}	t^{c}	10^{a}	14^{a}	4^{b}	$<1^{b}$
Total grasses	357^{a}	320^{a}	124^{b}	10^{c}	84^{a}	68^{b}	42^{c}	5^{d}
Total forbs	14^{c}	73^{a}	12^{c}	40^{b}	3^{c}	15^{b}	4^{c}	21^{a}
Gutierrezia sarothrae	54^{b}	77^{b}	157^{a}	143^{a}	13^{c}	16^{c}	54^{b}	74^{a}
Total vegetation	425^{a}	471^{a}	292^{b}	193^{c}	100	100	100	100

[1]Data were pooled across the first 3 years and last 3 years of study for trend comparisons as suggested by Holechek et al. (1999).
[a, b]Means within rows with different letters differ (P < 0.05).
t = trace

0.05). We will focus our discussion on standing crop trends over time for each stocking strategy concentrating on comparisons between the first and last 3 years of the study (Table 3).

Standing crop of total vegetation and total grasses showed no change (P > 0.05) on the lightly grazed rangeland, but declined (P < 0.05) on the moderately grazed rangeland when the last 3 years were compared to the first 3 years of the study (Table 3). Black grama standing crop increased on the lightly grazed rangeland, but decreased on the moderately grazed rangeland during the study period. Black grama is the primary decreaser perennial grass in the Chihuahuan Desert (Canfield 1939, Paulsen and Ares 1962). Dropseed (*Sporobolus* spp.) standing crop decreased (P < 0.05) on both rangelands. We attribute this decrease to below average precipitation in the 1994–1996 period. Dropseeds are less drought tolerant than black grama (Campbell 1929, Herbel and Gibbens 1996). Total forb standing crop increased (P < 0.05) on both rangelands in 1998–2000 compared to 1988–1990. Forbs in the Chihuahuan Desert are responsive to winter–spring precipitation. Winter–spring precipitation was higher in 1998–2000 than 1988–1990.

Broom snakeweed (*Gutierrizea sarothrae* Pursh), the primary poisonous plant found on both rangelands, showed no change (P > 0.05) in autumn standing crop on either rangeland when the last and first 3 years of study were compared (Table 3). Broom snakeweed is a short-lived, cyclic half-shrub that can cause abortion in livestock and has severely depressed productivity of perennial grasses on New Mexico rangelands (McDaniel et al. 1993). Populations of broom snakeweed are closely related to climatic conditions (Pieper and McDaniel 1990). Above normal autumn through spring precipitation favors broom snakeweed establishment. Broom snakeweed standing crop levels averaged nearly twice as high (P < 0.05) on the moderately grazed as on the lightly grazed rangeland.

Total grass, total forb, and black grama foliar cover averaged higher (P < 0.05) on the lightly grazed than the moderately grazed rangeland (Table 4). However, total shrub cover was higher (P < 0.05) on the moderately grazed rangeland. Most canopy cover components had significant interactions (P < 0.05) between stocking strategy and time period.

Generally, vegetation foliar cover (Table 4) showed the same trends as autumn standing crop for primary herbaceous components with a few exceptions. We cannot explain why total autumn standing crop of forbs increased (P < 0.05) between 1988–1990 and 1998–2000, but foliar cover showed no change (P > 0.05). We believe this is probably a sampling aberration.

Total shrub and honey mesquite foliar cover showed no changes (P > 0.05) during the period of study on either rangeland. Honey mesquite canopy cover on the lightly grazed range was only half (P < 0.05) that on the moderately grazed rangeland. This is explained in part by more intensive control of mesquite with herbicides on the lightly grazed rangeland prior to the initiation of our study.

Both herbaceous standing crop and foliar cover showed major changes (P < 0.05) in relative vegetation composition when the last and first 3 years of the study were compared (Tables 3 and 4). They were consistent in showing a shift to lower (P < 0.05) total grass and dropseed com-

Table 4. Average autumn vegetation foliar cover (%) and relative composition on lightly grazed (LG) and moderately grazed (MG) Chihuahuan Desert rangelands in south central New Mexico for the 1988–1990 and 1998–2000 periods.

Species or group	Vegetation Foliar Cover LG		Vegetation Foliar Cover MG		Relative Foliar Vegetation Composition LG		Relative Foliar Vegetation Composition MG	
	88–90	98–00	88–90	98–00	88–90	98–00	88–90	98–00
	(%)							
Aristida spp.	0.4^{a}	0.3^{a}	0.2^{a}	0.2^{a}	4^{a}	2^{a}	1^{a}	1^{a}
Bouteloua eriopoda	0.4^{a}	0.6^{a}	0.1^{b}	t^{b}	4^{a}	5^{a}	$<1^{a}$	$<1^{a}$
Erioneuron pulchellum	0.1^{a}	0.2^{a}	0.2^{a}	0.2^{a}	1^{a}	2^{a}	1^{a}	1^{a}
Sporobolus spp.	1.4^{a}	0.4^{c}	0.9^{ab}	t^{c}	13^{a}	3^{b}	4^{b}	$<1^{b}$
Total grasses	2.9^{a}	2.2^{a}	1.6^{b}	0.4^{c}	26^{a}	17^{b}	7^{c}	2^{d}
Croton pottsii	0.3^{a}	0.2^{a}	ta	t^{a}	2^{a}	1^{a}	$<1^{a}$	$<1^{a}$
Total forbs	0.4^{a}	0.4^{a}	0.2^{c}	0.5^{a}	4^{a}	3^{a}	1^{a}	2^{a}
Gutierrezia sarothrae	1.3^{b}	2.0^{b}	6.8^{a}	8.4^{a}	12^{b}	16^{b}	31^{a}	34^{a}
Ephedra spp.	0.2^{a}	0.2^{a}	0.3^{a}	0.3^{a}	2^{a}	2^{a}	1^{a}	1^{a}
Yucca elata	1.2^{a}	1.3^{a}	0.7^{a}	0.7^{a}	11^{a}	10^{a}	3^{b}	3^{b}
Acacia constricta	0.6^{b}	0.6^{b}	1.3^{a}	1.5^{a}	5^{a}	5^{a}	6^{a}	6^{a}
Prosopis glandulosa	4.5^{b}	6.2^{b}	11.2^{a}	12.6^{a}	41^{a}	48^{a}	51^{a}	52^{a}
Total shrub cover	6.5^{b}	8.3^{b}	13.5^{a}	15.1^{a}	59^{a}	64^{a}	61^{a}	62^{a}
Total vegetation cover	11.1^{b}	12.9^{b}	22.0^{a}	24.4^{a}	100	100	100	100

[1]Data were pooled across the first 3 years and last 3 years of study for trend comparisons as suggested by Holechek et al. (1999).
[a,b]Means within rows with different letters differ (P < 0.05).
t = trace

ponents on both rangelands and a higher forb component on the moderately grazed rangeland.

Rangeland ecological scores, based on the USDA-NRCS method and current New Mexico range site guides, averaged higher ($P < 0.05$) on the lightly than moderately grazed rangeland (Table 1). They showed an upward trend ($P < 0.05$) on the lightly grazed rangeland, but a downward trend ($P < 0.05$) on the moderately grazed rangeland (Table 2). Rangeland ecological condition scores on both rangelands showed considerable fluctuation among years (Table 2).

We believe our study provides support for the model of Dyksterhuis (1949) regarding rangeland vegetation responses to grazing and climate. However, we cannot reject the state-and-transition model of Westoby et al. (1989). They are not competing models. Both high mesquite foliar cover (13%) and lack of perennial grasses make it doubtful that meaningful improvement can occur in ecological condition on the moderately grazed rangeland through grazing management alone (Herbel et al. 1983). Mesquite control will be needed to restore this rangeland to a healthy condition as defined by the United States Department of Interior (2000).

Perennial grass plant survival percentages were higher ($P < 0.05$) for all 3 grasses [black grama, dropseeds, and threeawns (*Aristida* spp.)] evaluated on the lightly compared to the moderately grazed rangeland (Table 5). Most perennial grass mortality on both rangelands likely occurred during the period of below average precipitation in 1994–1996 (Table 2). During the summer of 1997 when above average rainfall occurred, most black grama plants on the lightly grazed rangeland showed green tops, but those on the moderately grazed rangeland remained black. Very few studies have evaluated perennial grass survival under different grazing intensities. In the Edwards Plateau of Texas, perennial grass survival during the 1950's drought was closely related to stocking rate (Young 1956). Lightly stocked pastures had 66% higher grass survival than those heavily stocked and 33% higher than those moderately stocked. Better photosynthetic capability and more extensive root systems of lightly grazed plants under stress are the primary explanations for this relationship. An additional explanation is better soil moisture conditions under light grazing due to more mulch and soil organic matter (Molinar et al. 2001).

Table 5. Percentages of live perennial grass plants on long-term lightly grazed (LG) and long-term moderately grazed (MG) Chihuahuan Desert rangelands in south central New Mexico in Autumn 1999.

	LG	MG
Grass species		
	--- (% live plants) ---	
Bouteloua eriopoda	80^a	10^b
Sporobolus spp.	23^a	5^b
Aristida spp.	67^a	12^b
Other grasses[1]	35a	15^b
Average	51^a	11^b

[1]Primarily Setaria leucopila and Muhlenbergia porteri.

Dropseed mortality was over 70% on both rangelands (Table 4). Other studies have shown that black grama is more drought resistant than dropseeds (Paulsen and Ares 1962, Wright and Van Dyne 1976, Herbel and Gibbens 1996). This may be explained by black grama having a more extensive root system and more capability to extract moisture from dry soils than dropseeds.

Forage utilization during the 13 year study period averaged 26% on the lightly grazed rangeland and 49% on the moderately grazed rangeland. Generally forage use levels in excess of 50% are considered heavy based on a review by Holechek et al. (1999). Heavy grazing is defined as a degree of herbage use that does not permit desirable forage species to maintain themselves (Klipple and Bement 1961). Grazing reached the heavy level only in the summer of 1995 on the lightly grazed rangeland, but was heavy to severe for 5 consecutive years (spring 1995 to spring 1999) on the moderately grazed rangeland. Black grama stubble height averaged 11.3 cm on the lightly grazed rangeland, but 5.6 cm on the moderately grazed rangeland during the 13 year study period. A minimum stubble height of 7.6 cm is recommended for maintenance of black grama (Valentine 1970). Dropseed stubble heights averaged 22.5 cm on the lightly grazed rangeland, but 11.2 cm on the moderately grazed rangeland. A minimum stubble height of 15.0 cm is recommended for dropseeds (Holechek and Galt 2000).

Our study is consistent with earlier studies by Canfield (1939), Paulsen and Ares (1962), and Valentine (1970) that light to conservative grazing intensities can be effective in maintaining and increasing forage production on Chihuahuan Desert rangelands dominated by black grama. Our study is also consistent with these studies in showing that heavy to severe grazing during drought can quickly degrade these rangelands. Our research shows the commonly used guideline of take half and leave half does not work well on arid and semi-arid rangelands. The problem with this guideline is that major destocking will be required in 50% of the years to avoid excessive use of primary grasses (Hutchings and Stewart 1953, Paulsen and Ares 1962, Martin 1975, Galt et al. 2000). In contrast, major destocking is only needed in about 2 years out of 10 when rangelands are stocked lightly. The difficulties of estimating forage production and buying and selling livestock make management for 50% grazing use a risky and unsound proposition. Improvements in forage production and rangeland health are unlikely and the probabilities of rangeland degradation and financial ruin are high unless the rancher is extremely savvy and capable of reacting quickly.

Summary and Conclusions

Our 13 year study (1988–2000) showed an upward vegetation trend on a lightly grazed rangeland while a downward trend occurred on an adjacent moderately grazed rangeland (Fig. 1). Various measures of vegetation change were used to monitor trend in our study.

Even though forage use was estimated to average 49% on the moderately grazed rangeland during the 13 year study period, a sharp downward trend occurred. The rancher attempted to keep livestock numbers in balance with forage supplies, but was unsuccessful in 5 of the 13 years studied. Although sharp reductions were made in cattle numbers during drought years, heavy to severe grazing use still occurred. By the last 3 years of study, palatable perennial grasses had been nearly eliminated (Fig. 1). Both brush control and seeding may be needed to obtain meaningful increases in forage production on this rangeland.

In contrast to the moderately grazed rangeland, the lightly grazed rangeland had a strong upward trend in ecological condition. This was primarily due to an increase in production of black grama during the last 3 years of study. Major adjustments in cattle numbers on the lightly grazed rangeland were only needed in 1994 and 1995 when it was completely destocked due to drought and lack of forage.

Our research indicates that severe grazing during drought greatly increases perennial grass mortality compared to light grazing. Rangeland retrogression in the Chihuahuan Desert can occur within 2 years when drought and severe grazing are coupled together. On the other hand, recovery from short-term drought can occur within 3 years if rangelands are destocked before excessive use occurs. Light to conservative grazing is important in non-drought years because it allows black grama to increase crown area and root growth (Canfield 1939, Paulsen and Ares 1962, Valentine 1970, Young 1980). Our study supports the recommendation by various researchers that grazing intensities on Chihuahuan Desert rangelands be kept at around 30 to 35% use of perennial grasses (Canfield 1939, Paulsen and Ares 1962, Valentine 1970, Young 1980, Holechek et al. 1994).

Our data show that a combination of information on precipitation, forage production, grazing intensity, livestock numbers, range condition, and range trend are needed for sound management decisions. We recognize that it is seldom possible to collect all this information due to limitations of money, labor, time, and technology. Light to conservative grazing is most needed where intensive monitoring is not possible or practical. This minimizes the risk of destructive grazing in drought years from failure to adequately destock. Recently, several range professionals have advocated the use of a 25% harvest coefficient in arid and semi-arid areas when stocking rates are set to reduce risk and facilitate range improvement (Lacey et al. 1994, Johnston et al. 1996, White and McGinty 1997, Ward 1999, Galt et al. 2000). Our research on Chihuahuan Desert rangelands supports this recommendation.

As a final point, we believe our study contradicts Donahue's (1999) viewpoint that livestock grazing is not sustainable on arid lands receiving less than 30 cm of annual precipitation. During the 13 year study period, the lightly grazed pasture improved from late seral to climax ecological condition.

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J. Range Manage.
56: 140-145 March 2003

A digital photographic technique for assessing forage utilization

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Abstract

Changes in forage utilization have been difficult to measure non-destructively without some level of subjectivity. This subjectivity, combined with a lack of reproducibility of visual estimates, has made forage utilization measurement techniques a topic of considerable discussion. The objective of this study was to develop and test the accuracy and repeatability of an objective, computer-based technique for measuring changes in plant biomass. Digital photographs of target plants acquired before and after partial defoliation were analyzed using readily available image analysis software. Resulting data were used to develop a simple linear random coefficient model (RC) for estimation of plant biomass removed based on the area of the plant in the photo. Sample collection took approximately 20 minutes/plant for alfalfa (*Medicago sativa* L.). Analysis of images took another 60 to 90 minutes. Regression analysis gave an R^2 of 0.969 for predicted vs. observed plant weights. Testing this model using 10 alfalfa plants yielded weight estimates of defoliated plants accurate to within +/- 8.5%. The advantage of the RC model is its ability to use easily obtained coefficients from simple linear regression models developed from each plant in a way that accounts for the lack of independence between samples within an individual plant. The technique described here offers an objective and accurate method for measuring changes in plant biomass with possible applications in ecology, botany, and range science. In particular, application of this technique for estimating forage utilization may improve accuracy of estimates and, thereby, improve range management practices.

Key Words: image analysis, alfalfa, *Medicago sativa*, random coefficient model.

Resumen

Los cambios en la utilización de forraje han sido difíciles de medir en forma no destructiva sin un grado de subjetividad. Esta subjetividad, combinada con la carencia reproducción de las estimaciones visuales, ha hecho que las técnicas de medición de utilización de forraje sea un tópico de considerable discusión. El objetivo de este estudio fue desarrollar y probar la certeza y repetibilidad de una técnica computacional objetiva para medir la biomasa vegetal. Fotografías digitales de plantas de interés tomadas antes y después de ser sujetas a una defoliación parcial fueron analizadas utilizando programas de computación ya disponibles para el análisis de imágenes. Los datos resultantes fueron utilizados para desarrollar un modelo lineal simple de coeficiente aleatorio (RC) para estimar la biomasa vegetal removida basándose en el área de la planta en la fotografía. La colección de la muestra tomó aproximadamente 20 minutos/planta de "Alfalfa" (*Medicago sativa* L.), el análisis de las imágenes tomo otros 60 a 90 minutos. El análisis de regresión produjo una R^2 de 0.969 para los pesos de planta predichos contra los observados. La prueba de este modelo usando 10 plantas de "Alfalfa" produjo estimaciones de peso de las plantas defoliadas con una certeza dentro de +/- 8.5%. La ventaja del modelo RC es su capacidad para usar coeficientes fácilmente obtenidos a partir de modelos de regresión lineal desarrollados de cada planta en una manera que toma en cuenta la falta de independencia entre muestras dentro de una planta individual. La técnica descrita aquí ofrece un método objetivo y certero para medir cambios en la biomasa de las plantas con posibles aplicaciones en ecología, botánica y manejo de pastizales. En particular, la aplicación de esta técnica para estimar la utilización de forraje puede mejorar la certeza de las estimaciones, por lo tanto, mejorar las prácticas de manejo de pastizales.

Measurement of current-year's forage production that is either consumed or destroyed by grazing animals (Society for Range Management 1974) is critical for successful rangeland management. Despite the importance of accurately measuring range utilization, methods currently available have various constraints that limit their usefulness (Holechek et al. 1989). Techniques that allow greater accuracy and can detect small differences in animal use are extremely tedious and labor intensive. These latter problems severely limit quantitative research because large sample sizes are required to obtain accurate forage use estimates (Estell et al. 1998). The objective of the work described in this paper was to develop a rapid, accurate, and repeatable quantitative technique for objective assessment of forage utilization. We also desired a technique that was readily available to most researchers at reasonable costs. To accomplish this task, we focused on recent technological advancements in digital photography and image analysis. The photographic aspect of this method adds a level of flexibility and reliability not found in other methods.

The authors would like to thank 2 anonymous reviewers for their constructive comments. Field assistance from David Hu and Andrine Morrison is greatly appreciated.

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Manuscript accepted 25 May 02.

Photographs provide a permanent record that allows an objective estimate of the area, and through modeling, the mass of a plant to be calculated.

Materials and Methods

Field Technique

The field component of this study was conducted at the USDA, Agricultural Research Service, Sheep Research Facility located at the La Tuna Federal Correctional Institute in Anthony, Tex. Alfalfa (*Medicago sativa* L.) was used because of its importance as a forage plant. Fifty alfalfa plants were randomly selected from a 10 x 2-m plot. Each plant was transplanted to a 5-gallon bucket. Transplanting each plant allowed us to deal with developing the technique on a plant-by-plant basis with no interference from neighboring plants or other objects. To separate the plant from the background, a sheet of white, dry-erase board was placed behind, but not touching, the plant (Fig. 1A). Plant identification, date, sample number, and photo angle were recorded on the dry-erase board. A ruler attached to a wire was placed to the side of the plant on a plane bisecting the midpoint of the plant. Each ruler was held in place by inserting the attached wire into the soil. A second ruler was placed perpendicular to the first, also on a plane bisecting the plant's midpoint. These rulers served to calibrate the image and to establish 0 and 90° reference angles. To improve calibration accuracy, the rulers were trimmed to a total length of 10 cm, eliminating the need to see the marks on the ruler.

A digital camera (Kodak® DC260) was used to photograph the plants. Two photographs were taken at each sampling stage (sample 0-k) with the first 2 taken prior to defoliation (sample 0). The first photograph of each pair was taken at the midpoint of the plant height and width from a direction minimizing shadows. The second was taken at 90°, on a horizontal plane, from the first. The white backdrop was also rotated at each step.

Plants were hand-defoliated in 5 steps. Approximately 20% of the total plant weight was removed and collected as a sample during each step. As each sample was collected, the sample number was recorded on the backdrop and the plant rephotographed. Succeeding photos were taken from as close to the same position as possible. Samples collected at each step were bagged and labeled separately. During the last defoliation step, all remaining above ground tissue was removed. Each sample was dried at 60° C for 24 hours prior to being weighed to the nearest 0.5 g. The weight of each defoliation was recorded and then summed to determine total weight of the plant.

Image Analysis

Jandel's SigmaScan Pro® 3.0 was used to analyze the digital images. Any image analysis software could be used provided it has something approximating the following capabilities: image cropping, calibration of scale, color/black and white/contrast transforms, intensity selection procedures, and some form of data reporting program. These are used to prepare the image of the plant for areal measurement. Image cropping helps isolate the target image from incidental objects. This will become important as the technique evolves for use in the field. Once the image is adequately prepared, the program counts pixels of various values that correspond to the image. These pixels are then transformed to area based on the measurement of a known distance on the image, in this case the 10-cm ruler, to the number of pixels contained in the length of the image of the ruler. Color/black and white/contrast transforms and intensity selection procedures enhance isolation and measurement of the target image (Fig. 1B, C, and D). In our method, the color image was transformed to black and white (grayscale) due to the program we used being better able to delineate the image in black and white. Once the measurements are made, such that a calculation of area for each image is available, the data can be copied into a spreadsheet for further analysis.

Sample weights and photographic areas were converted to percent weight remaining and percent area remaining, respectively. We used a mean calculated from the percent remaining areas for angles 0° and 90° to address the 3 dimensional aspect in a 2 dimensional form. Forty plants were used to develop a statistical model and 10 plants to test the model. To test for repeatability of the image analysis, we calculated the area for 1 plant image 10 times. To test sampling precision, we calculated the mean deviation from the desired 20% defoliation sample size and standard deviation of this mean for the samples taken from the 40 plants used to build the model.

Model Building

A statistical model was constructed to provide estimates of individual plant utilization, specifically for this particular variety of alfalfa (Malone) at this particular stage of growth. The random coefficient (RC) model was used and can be written as [$y_{ij} = \beta_0 + s_i + (\beta_1 + d_i)x_{ij} + e_{ij}$, i=1, ..., n and j=1, ..., *k*] where y_{ij} is the percentage of the i[th] plant remaining after the j[th] sample is removed, x_{ij} is the remaining area covered in the photograph of the ith plant after the jth sample is removed, β_0 is the y-intercept, β_1 is the slope, and s_i, d_i, and e_{ij} are random effects in the model associated with the random deviation of the i[th] plant's intercept from the intercept β_0, the random deviation of the i[th] plant's slope from the slope β_1, and random error, respectively (Graybill 1976).

The first step in building the RC model is to estimate a simple linear regression (SLR) equation for each plant. Each SLR equation describes the straight-line relationship between the percentage of remaining plant (y) and the percentage of remaining area covered in the photograph (x) for a single plant. In general notation, let b_{0i} and b_{1i} denote the estimated y-intercept and slope for the i[th] plant (i = 1,..., n). Computations were performed using fifteen significant digits and rounded to one for illustration purposes. The estimated SLR equation for the i[th] plant is $Y_{ij} = b_{0i} + b_{1i}x_i$.

A small subset of the data set (n = 4, k = 5) is given in Table 1 to use in illustrations of the statistical computations. The estimated SLR equations and associated sums of squared residuals for each of the 4 plants in Table 1 are reported in Table 2.

Table 1. Example data used to demonstrate statistical methods.

Plant	Sample	Area remaining in photograph	Weight of remaining plant
		(%)	(%)
1	1	87	93
1	2	67	77
1	3	48	59
1	4	30	42
1	5	13	24
2	1	91	93
2	2	71	77
2	3	52	61
2	4	27	38
2	5	14	25
3	1	89	94
3	2	72	78
3	3	50	60
3	4	30	41
3	5	19	28
4	1	86	92
4	2	67	76
4	3	47	58
4	4	27	39
4	5	13	24

Table 2. Estimated Simple Linear Regression (SLR) equations and Sum of Squared Residuals relating the percentage of remaining plant (y) to the percentage of remaining area covered in the photograph (x) for each plant in Table 1.

Plant	SLR Equation	Sum of Squared Residuals
1	y = 13.25 + 0.9337x	6.9594
2	y = 13.77 + 0.8829x	4.7088
3	y = 12.15 + 0.9241x	7.5185
4	y = 13.24 + 0.9283x	4.9426

The y-intercept and slope of the RC equation are estimated by computing the sample averages of the estimated individual plant y-intercepts and slopes, respectively. The estimators for the y-intercept and slope can be written as

$$\hat{\beta}_0 = \frac{1}{n}\sum_{i=1}^{n} b_{0i} \quad (1)$$

and

$$\hat{\beta}_1 = \frac{1}{n}\sum_{i=1}^{n} b_{1i} \quad (2)$$

respectively. For our example,

$$\hat{\beta}_0 = \frac{1}{4}\sum_{i=1}^{4} b_{0i} = (13.2+13.8+12.1+13.2)/4 = 13.1$$

and $\hat{\beta}_1 = \frac{1}{4}\sum_{i=1}^{4} b_{1i} = (0.93+0.88+0.92+0.93)/4 = 0.92$

Thus, the estimated equation for the RC model is $\hat{y}_{ij} = \hat{\beta}_0 + \hat{\beta}_1 x = 13.1+0.92x$ for this example.

The estimated mean of y at a given value of x (say x*) is

$$(\hat{y} \mid x = x^*) = \hat{\beta}_0 + \hat{\beta}_1 x^* \quad (3)$$

For the example, an estimate of the percentage of a plant remaining that was observed to have, say, 80% of the area remaining in a photograph of the plant after it was browsed by an animal, is y given x = 80 or $(\hat{y} \mid x = 80) = \hat{\beta}0 + \hat{\beta}1 (80) = 13.1 + 0.92x = 86.5$.

Results and Discussion

Theoretically, the limit for detection of biomass removal should correspond to the area of the photo covered by a pixel given that the tissue removed is on a plane visible to the camera, i.e., not hidden by intervening tissue. This plane of visibility is probably the most important source of variation in the individual plant models. Photographing plants from perpendicular directions and taking the mean area of the 2 images helped to reduce variation incorporated into the model by the 3-dimensional shape being reduced to 2 dimensions during analysis. Estimates of the remaining percentages of plant weights were accurate to +/–21% using the 0° angle photographs and to +/–17% using the 90° angle photographs, but were accurate to +/- 8.5% using the mean of the 0° and 90° angle photographs. The mean area for the repeated images was 676 cm^2 (SD = 21.61, CV = 3.19, n = 10). The basic premise, that a pair of photographs taken at perpendicular angles can adequately model the 3-dimensional plant, seems to hold up well.

Problems encountered were the inability to distinguish plant tissue from background clutter, poor image quality, and increasing area with decreasing biomass. The backdrop solved the background clutter problem. Using a digital camera and image manipulating software allows the operator to manipulate image factors and does much to solve image quality problems. The area-biomass problem is typically the result of allowing the background screen to contact the plant or photographing the plants under windy conditions thereby changing the apparent area between photographs. These 2 factors are the main contributors to the plane of visibility problem mentioned above. To ensure the repeat positioning of the camera for sequential shots, one could use 2 tripods placed at right angles to the plant and simply move the camera between the tripods. The use of quick release heads on the tripods would facilitate this approach. With SigmaScan Pro® 3.0, the set threshold routine is a potential source of subjectivity. Carefully setting the threshold values in the first image so that plant tissue is maximized and extraneous material is minimized and then holding this value constant throughout the series of images will minimize the subjectivity inherent in this step. Figure 1D shows an example of a threshold setting where plant tissue is highlighted, but shadows and grass stems are not.

There are additional considerations if film is used. In a previous trial, we used Kodachrome, 64 slide film. Upon return of the processed slides, they were digitized with a Nikon Coolscan® slide digitizer. This gave us good control over the image quality with respect to setting up the image for further analysis. Prints could possibly be used with a flatbed scanner, but the superior resolution, for a given film speed, of slides vs. prints may argue against the use of print film. This difference in resolution is due to the inherent loss of information that occurs when an image is transferred to a different medium, i.e., film negative to paper. It is possible that this loss of resolution would be too small to have an effect on this technique. A fast film (ISO of 200 or more) used with flash would enable working during periods of light to moderate winds. The use of a flash should help reduce problems created by shadows. Depth of field should be maximized so that the entire image of the plant is as sharp as possible.

Time investments in this technique are somewhat longer than with previous methods listed in Table 3, but the improved results offset the increased time invested. Collecting samples and photographing alfalfa plants took an average of 20 minutes/plant. A large part of the post-sampling time spent depends on the camera used. Digital cameras provide usable images immediately. Turn-around time for development of film is dependent on whether the film is sent to a lab or developed in house. Once slides, or digitized images, are available, the process takes 3 to 5 minutes per image to calculate the variables of interest. This data is then transcribed to spreadsheet form and appropriate statistical analyses completed. Training of inexperienced individuals could probably be done in 2 sessions of roughly 4 hours each, an hour each for photography, digitizing, image analysis, and data collection plus some time to practice the technique. Once simple linear regression equations are computed for each plant, construction of the random coefficient model is relatively easy.

Table 3. Comparison of methods for estimating utilization.

Method	Time	Accuracy
	(days)[a]	(%)
Digital Photographic	4	± 8.5
Ocular by Plot[b]	2	+ 19
Ocular by Plant[b]		+ 2
Leaf Length[b]		+ 16
Plant Count[b]		+ 26
Height/Weight Ratio[c]		+ 10-25

[a]Time includes model building and training.
[b]Pechanec and Pickford (1937) (these values are means).
[c]Clark (1945).

Statistical analysis of this data set using simple linear regression across all plants would seem to be an intuitive approach. An important assumption associated with simple linear regression (SLR) is that the

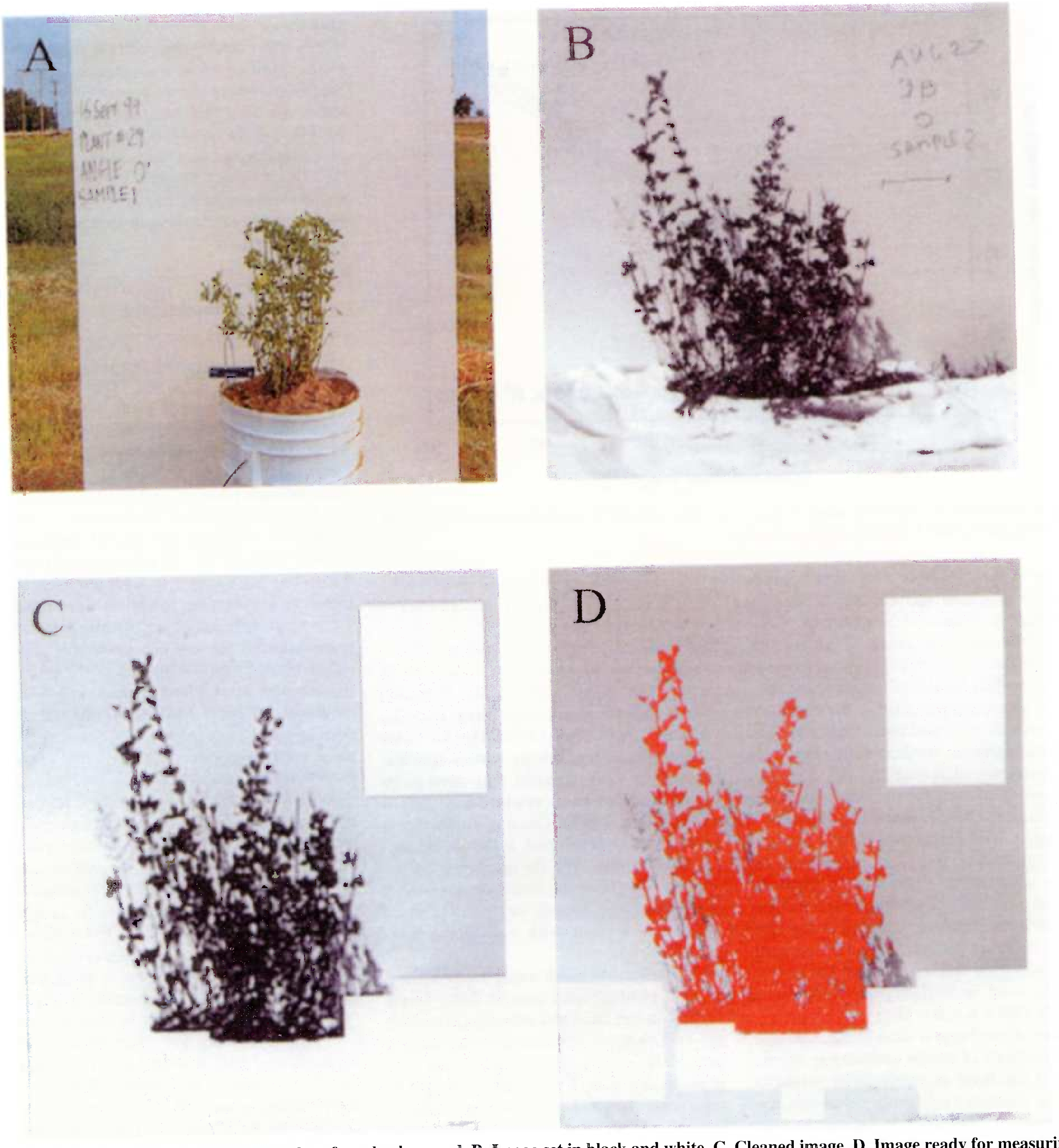

Fig. 1. A. Apparatus for separating plant from background. B. Image set in black and white. C. Cleaned image. D. Image ready for measuring.

random variable (y) at each value of x is independent of the random variable y at any other value of x. In the present work, sequential samples were taken from each plant resulting in measures of biomass (y) at various values of area (x) that are not independent of each other. The RC model addresses the problem of a lack of independence by using the line produced for each plant by simple linear regression as the attribute of interest. From a statistical perspective, this approach is preferred because the estimates are more precise and because the sources of variability can be partitioned and examined to improve future models.

The RC model fit to the data from 40 of the alfalfa plants resulted in the equation [$Y_{ij} = 9.06 + 0.976x$]. Figure 2 shows the estimated and observed percentages of plant remaining for sample points from 10 plants not used in constructing the model. There is an increased sensitivity at lower levels of defoliation. The greater sensitivity is advantageous due to desired utilization levels, which usually requires leaving more than 50% of the plant.

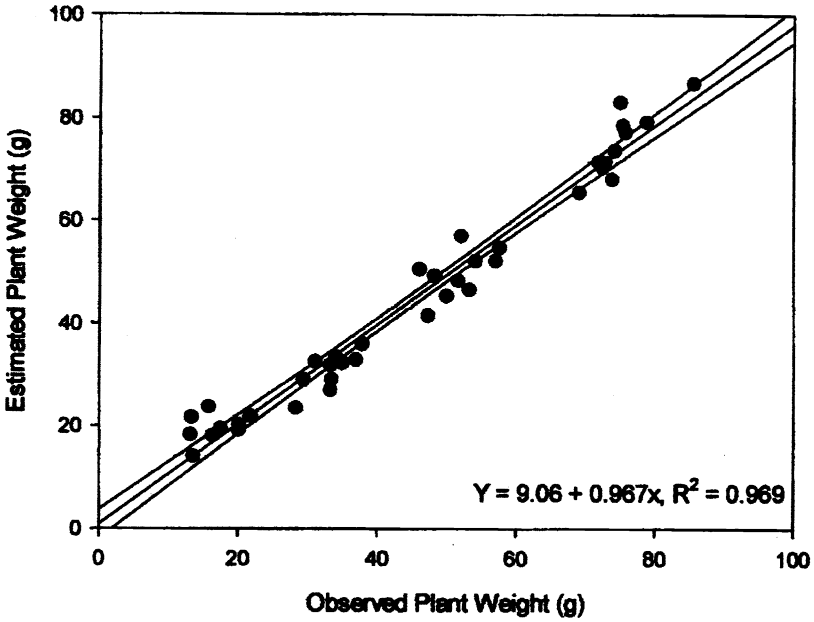

Fig. 2. Estimated vs. observed plant weight remaining with 95% confidence intervals for 10 alfalfa plants with 4 samples from each plant.

The optimal sample allocation between number of plants and number of samples per plant is dependent on plant morphology. However, because of statistical assumptions of normality, we recommend no fewer than 30 plants. The optimal number of measures per plant is dependent on the researcher's experience with the sample/photographic methodology. However, for purposes of fitting the RC model, a minimum of 4 measurements per plant including the whole plant measurement is required. The researcher must conscientiously attempt to select samples at the same x-values for each plant to meet statistical assumptions of the model. For our samples, the mean deviation from the ideal 20% intervals between areas of consecutive samples within a plant for the 40 plants used in building the model was 12.5% (SD = 6.2, n = 160).

One of the biggest drawbacks with current methods of forage and browse utilization is the level of subjectivity required. Ocular estimates rely on the experience of the observer and may be subject to individual bias, particularly if the observer is not well trained or fails to periodically check his observations against a standard (Bement and Klipple 1959). Height/weight methods generally perform well, but are dependent on plants used to develop the model being similar in morphology to the plants being estimated (Clark 1945). The technique described in this paper incorporates aspects of several methods. It is similar to ocular-estimate-by-plant and height/weight methods in that individual plants are used as the basic units and a weight/area relationship is developed (Lommasson and Jenson 1938, Cook and Stubbendieck 1986). The digital-photographic method minimizes subjectivity through the use of photographs. Repeated measurements of an image gave a coefficient of variation of 3.19%. Due to variation in plant morphology across species, seasons, or sites, a model may need to be developed for each application (Caird 1945, Clark 1945). Once a model for a given plant is developed, it should be useful indefinitely. We do not know at the present time what the limits on usefulness are for a given model, say alfalfa, when applied to a plant with a different morphology.

Collection of plant samples and their related photographs can be done fairly rapidly in the field and subsequent modeling and analysis completed in the laboratory. Additionally, photographs from sites to be analyzed for forage utilization can be taken and analyzed at a time convenient to the individual doing the assessment. A series of forage conditions could be photographed at intervals throughout the season and an analysis of season-long changes could be carried out. This technique will be difficult to use on large shrubs or trees due to the limitations of harvesting the entire plant for modeling. Estimates of weight/unit area may allow the use of this method for large shrubs or trees although indirect methods are probably of more value (Bonham 1989). Also, this method has not yet been tested on grasses or woody plants. Any situation where individual plants can be delineated in the field of view will probably work. Situations where plants are in close proximity, such as turf, may be problematic. As software of this type develops, the use of variation in color will likely improve the ability to differentiate specific targets and thereby improve the utility of digital-photographic methods such as the one presented here.

Conclusions

The digital-photographic method described herein accurately estimated the weight of individual alfalfa plants at sequential defoliation episodes to within ± 8.5%. The weight values were calculated from paired perpendicular photographs taken of each plant at each level (0, 20, 40, 60, 80, and 100%) of defoliation. Time needed to complete the model building varied from 22 to 32 hours total time depending on familiarity with techniques. Once an appropriate model is developed for a plant species, objective estimates of plant material present can be readily calculated based on photographs of the plant. Before and after photographs will give estimates of plant biomass removed, or remaining, if photographs are obtained in short enough temporal intervals that plant growth or leaf abscission does not become a confounding factor. Within this context, plant phenology should not affect estimates. The use of a digital-photographic method for estimating plant biomass lost to herbivores has applications in agriculture, ecology, and other fields. As image analysis technology improves, the applicability and accuracy of techniques such as this will improve. One aspect in particular need of improvement is the ability to separate target plants or groups of plants from background objects. For most shrubs and forbs in arid and semiarid environments that have a random or regular distribution, the problem associated with plant separation should be minimal. In all cases, the use of blocking objects, such as the backing board used here, will be needed to separate the plant from its background. The use of readily available computer technology and photographic equipment will decrease the subjectivity and increase the accuracy of field measurements of plant geometry and associated losses due to herbivory and/or other factors.

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J. Range Manage.
56: 146-151 March 2003

An index for description of landscape use by cattle

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Abstract

Understanding the role of landscape diversity in livestock distribution patterns is an important consideration for design of effective grazing systems. The objective of this study was to develop and evaluate a Distribution Evenness Index (DEI) based on the Shannon-Wiener index to characterize cattle distribution patterns for a heterogenous landscape within a given period of time. Observations of diurnal behavior of beef cattle (*Bos taurus*) were made in grassland, wooded, and riparian habitats within a fenced landscape from March to October 2000 at a farm in north-central Alabama. The DEI was calculated based on observation records at different time intervals (15-, 30-, and 60-min) and different levels of grassland habitat subdivision (18-, 9-, and 6-zones). Comparisons of calculated DEI values were made among different habitat types, observation intervals, landscape subdivision levels, and daytime periods. Annual DEI means indicated low evenness of cattle distribution in riparian (0.517) and wooded habitats (0.606), and consistently high evenness in the grassland habitat (0.860). Although grazing activity in the grassland habitat was uneven between different daytime periods (0.565 to 0.679), when combined for the total daytime period, grazing activity in the grassland habitat had a high evenness value (0.855). Relative stability of the DEI calculated between selected spatial and temporal scales in this study indicated that the index may be useful for comparison of evenness of livestock habitat use and grazing patterns between different studies at similar spatial and temporal scales.

Key Words: beef cattle, diurnal grazing behaviors, location choice, distribution evenness, riparian areas

Resumen

Entender el papel de la diversidad del paisaje en los patrones de distribución del ganado es de considerable importancia para el diseño de sistemas de apacentamiento efectivos. El objetivo de este estudio fue desarrollar y evaluar in Índice de Uniformidad de Distribución (DEI) basado en el índice de Shannon-Weiner para caracterizar los patrones de distribución del ganado en un paisaje heterogéneo dentro de un periodo de tiempo dado. Se hicieron observaciones del comportamiento diurno del ganado para carne (*Bos taurus*) en hábitats de zacatal, boscoso y ribereño, las observaciones se realizaron de marzo a abril del 2000 dentro de un paisaje cercado en una granja de la región norte-centro de Alabama. El DEI fue calculado en base a los registros de observación a diferentes intervalos de tiempo (15, 30 y 60 min) y diferentes niveles de subdivisión del hábitat de zacatal (18, 9 y 6 zonas). Se realizaron comparaciones de los valores calculados del DEI entre diferentes tipos de hábitat, intervalos de observación, niveles de subdivisión del paisaje y periodos del día. Las medias anuales del DEI indicaron una baja uniformidad de la distribución del ganado en los habitats ribereño (0.517) y boscoso (0.606) y una uniformidad consistentemente alta en el hábitat de zacatal (0.860). Aunque la actividad de apacentamiento en el hábitat de zacatal fue desuniforme entre los diferentes periodos del día (0.565 a 0.679) cuando se combinaron para el total del periodo del día, la actividad de apacentamiento en el hábitat de zacatal tuvo un valor de uniformidad alto (0.855). La estabilidad relativa del DEI calculada entre las escalas espaciales y temporales seleccionadas en este estudio indicó que el índice puede ser útil para la comparación de la uniformidad del uso del hábitat por el ganado y los patrones de apacentamiento entre diferentes estudios en escalas espaciales y temporales similares.

Grazing distribution patterns affect optimal forage utilization, nutrient recycling, and ultimately, pasture persistence and grazing capacity. Thus, an important principle of grazing management is to maintain an even distribution of grazing animals within a grazing unit or area (Vallentine 2001). In addition, animal agricultural production practices are being increasingly scrutinized for their impact on water quality throughout the USA (Martin 1997). Therefore, livestock distribution is a fundamental concern in grazing system design. This is especially true for grazing units that include wooded riparian areas, since cattle have been reported to spend more time near shade and water sources (Blackshaw and Blackshaw 1994).

Multiple regression (Senft et al. 1983), probability distributions (Arnold and Maller 1985), and inverse Gaussian distribution function (Pickup 1994) have been used to predict or measure livestock grazing distribution patterns. A drawback to these approaches is that these models cannot be transferred from 1 site to another since relationships between distribution patterns and environmental characteristics vary from location to location (Bailey et al. 1996). The objective of this study was to develop an index based on modification of the Shannon-Wiener index (Shannon and Weaver 1949) by which evenness of the distribution patterns of cattle location choice and behaviors could be easily quantified within a heterogeneous landscape over a given period of time. Sensitivity and stability of the distribution evenness index was tested at different temporal and spatial scales.

The authors wish to thank Mr. James Glenn, Glendale Farms, Moulton, Ala. for generously allowing access to his property. We also thank Mr. Rick Zellmer, GIS Specialist, USDA-NRCS, Auburn, Ala. for assistance with map development.

Manuscript accepted: 15 Jun. 02.

Materials and Methods

Description of study site

The study was conducted between March and October 2000 at Glendale Farms, close to the town of Moulton (196.6 m, 34°29'N, 87°18'W) in the Flint Creek Watershed of north-central Alabama, USA. The average annual temperature is 13 to 16°C. Average annual precipitation is 925 to 1,400 mm with maximum in midwinter and midsummer, and minimum in autumn. Stream discharge is generally greatest in late winter and spring in response to precipitation. Precipitation is generally adequate for forage growth, however, dry periods early in summer and in autumn can reduce biomass production. Rainfall during the study period ranged from a high of 220 mm in April to a low of 0 mm in October (Fig. 1). Total rainfall for the study period was 257.3 mm lower than the previous 30-year average.

The studied landscape was fenced to about 3.3 ha in rectangle and was part of a larger grazing system that used rotational stocking. A second-order stream (Sheats Branch) flowed through the studied landscape (Fig. 2). The producer had an 80-head beef cow-calf (*Bos taurus*; Hereford) herd that was allowed yearlong access to the stream. During observation periods, stocking density of the studied landscape averaged 5 AU ha^{-1} (20 total head) during the cool season (October to April) and 4 AU ha^{-1} (17 total head) during the warm season (May to September).

Three habitat types were defined within the studied landscape as riparian (stream, streambanks, and streamside woods), grassland (open pasture area), and wooded (wooded areas along fence line and drainage way). The area ratio of different habitat types was 1 (wooded) : 1.6 (riparian): 6 (grassland). Ground cover composition was quantified in both the grassland and riparian habitats using a point sampling technique (Buckner 1985). Endophyte-infected tall fescue (*Fescuta arundinacea* L.) was the predominant vegetation cover (84%) in the grassland habitat of the studied landscape; common bermudagrass (*Cynodon dactylon* L.) contributed up to 11% of the grassland vegetation cover. Measurements indicated uniform fescue production and utilization throughout the grassland habitat (Zuo 2001). Sycamore (*Platanus occidentalis* L., 54.3%) and oak (*Quercus* sp., 19.8%) were the dominant overstory species in the 5- to 10-m wide wooded portions of the riparian habitat; riparian overstory cover averaged 48% in winter and 84% in summer. Ground cover of the riparian habitat understory was dominated by the combination of litter (41%) and bare ground (28%). The total vegetative portion of the understory ground cover averaged 21% during the study period; tall fescue comprised approximately 40% of the total understory vegetation cover.

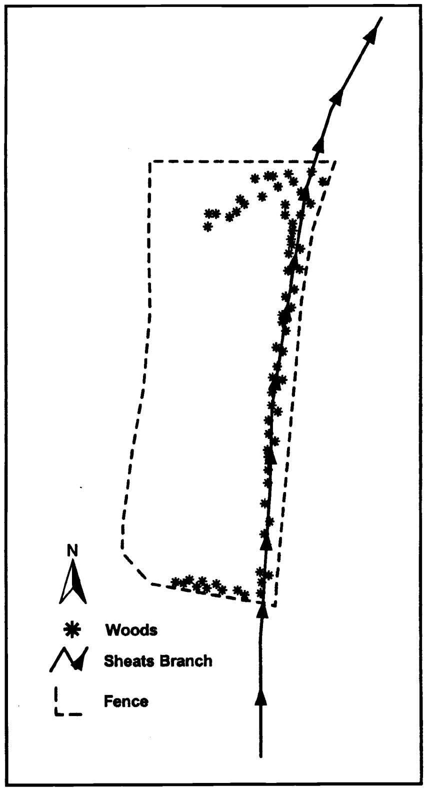

Fig. 2. Map of the studied landscape (3.3 ha), Glendale Farms, north-central Ala.

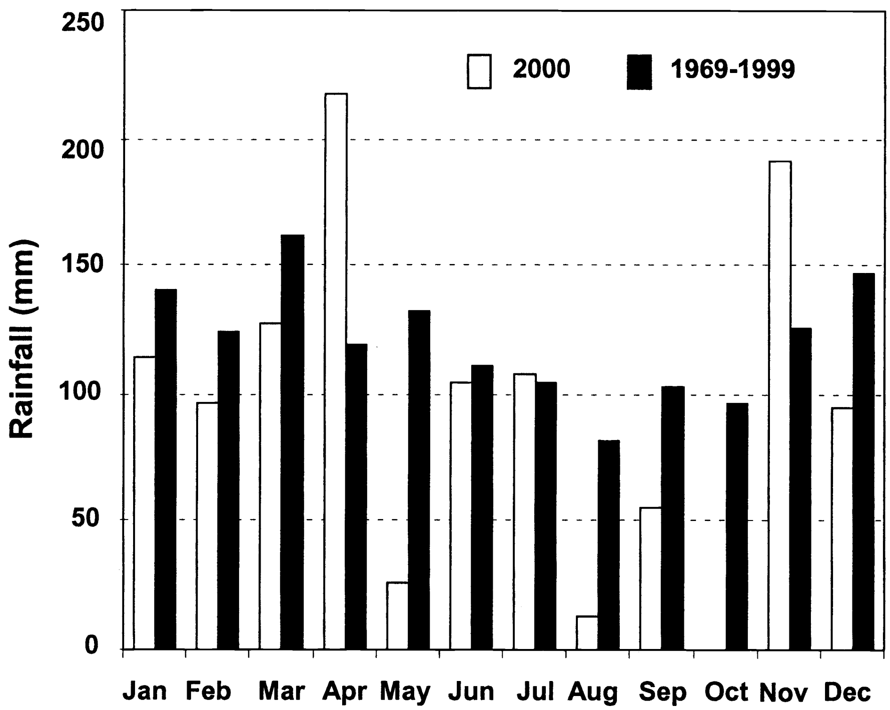

Fig. 1. Monthly rainfall during 2000 compared to the previous 30-year average, north-central Ala.

Observation of cattle behavior

Two-day diurnal observations of cattle behavior were made in March 2000; 1-day diurnal observations were made in May, July, August, and October 2000. From daybreak to dark, observations of weather conditions and cattle behavior were conducted at 15-min intervals with the assistance of binoculars from a convenient point that avoided disturbance of cattle. Data recorded during observations included: temperature, wind direction (Table 1), total number of head at each location, and activities of individual animals, such as grazing, lying, and loafing. Grazing activity represented times when cattle were harvesting and masticating forages; lying activity represented times when cattle were lying down at a given location; loafing activity represented activities other than grazing and lying, such as moving, standing, itching, and playing. The location, numbers, and behavior categories of cattle were recorded on a landscape map for each time interval during the observation periods; those maps were referred to as distribution plots. Total time was calculated as the sum of time cattle spent in the riparian habitat (including the stream), the grassland habitat, and the 2 areas of wooded habitat. Grazing time, lying time, and loafing time combined represented the total time period of the observation. The percentage of cattle participation in each activity within each habitat type was calculated. Based on the record of 15-min interval observations, 30- and 60-min-interval records were generated by deletion of 1 or 3, 15-min intervals in the calculation.

Calculation of the Distribution Evenness Index

For each distribution plot recorded at a given time interval, the total landscape area was subdivided into zones by overlaying a transparent zone-subdivision of the landscape on each distribution plot. The transparent overlay had 5 zones evenly delineated in the riparian habitat, 18 zones in the grassland habitat, and 3 zones in the 2 wooded habitats within the studied landscape. For the grassland habitat only, transparent overlays with 9- and 6-zone subdivisions were also applied separately to each distribution plot. Based on the summary record of cattle numbers and behavior categories for each zone at a given period of time, an index of cattle distribution evenness was calculated by a modification of the Shannon-Wiener index (H'). The information parameter H' was defined as:

$$H' = -\sum_{i=1}^{Z} p_i \ln p_i \qquad (1)$$

Where p_i = the proportion of total number or behavioral categories of beef cattle in the ith zone;

Z = total number of zones studied.

For zones without a record of any category of behavioral activity, 0.001 was assigned to make the calculation mathematically feasible. The statistic H' was then standardized for the number of zones involved (Z) to achieve the Distribution Evenness Index (DEI):

$$\mathrm{DEI} = H'/\ln Z = (-\sum_{i=1}^{Z} p_i \ln p_i)/\ln Z \qquad (2)$$

The Shannon-Wiener index was initially developed for human communication theory (Shannon and Weaver 1949) and has been widely applied in ecology as a measure of species diversity. Two assumptions must be satisfied to use the index for species diversity measurement: (1) individuals are randomly sampled from an 'infinitely large' population and (2) all species from a community are included in the sample (Kent and Coker 1992). Although the original purpose of the Shannon-Wiener index was to describe many types of human behavior, the DEI modification should be suitable to describe the distribution of cattle location choice since cattle behavior is a continuous process and the number of subdivision zones is fixed for a given area studied.

To simplify the mathematical explanation of the DEI, suppose there are only 2 zones within a grazed landscape. When the 2 probabilities of cattle choice of each zone are equal, the DEI is largest and reduces to 0 when 1 zone's freedom of choice is gone. If there are many, rather than 2 zones, then the DEI is largest when the probabilities of the choices of each zone are as near to equal as possible during a given period of time, namely, cattle spend nearly identical time in each zone. On the other hand, if the choice of 1 zone has a probability near 1 so that all the other choices have probability near 0, the indication is that the cattle's choices are heavily influenced toward one particular zone or cattle have little freedom of choice. In that case, the DEI does calculate to have a very small value, i.e., the distribution evenness is low.

Comparisons at different temporal and spatial levels

The Distribution Evenness Index (DEI) was calculated at different time intervals (15-, 30-, and 60-min) and different subdivision levels (18-, 9-, and 6-zone) in the grassland habitat for both total activities and categorized activities. When total activities were taken into account, the DEI represented the evenness patterns of location choice or distribution within the grassland habitat. The DEI was also calculated based on the 15-min interval data for cattle location choice in different habitat types. To describe the distribution pattern of grazing behavior in the grassland habitat during daylight, the DEI was also calculated based on the 15-min interval data for morning (before 1100 hours), midday (1100 to 1300 hours), afternoon (1300 to 1700 hours), and evening (after 1700 hour) periods.

Table 1. Predominant weather conditions for behavior observation periods, north-central Ala, March to October 2000.

Date	Sunrise	Sunset	High temp.	Low temp.	Weather conditions
	(h)	(h)	(°C)	(°C)	
9 March	0606	1749	13.3	3.3	Cloudy skies, strong wind from 0600 to 1400 hours with one and one-half hour rain beginning at 0830 hour; remaining periods were sunny
10 March	0604	1750	12.7	3.3	Sunny before 0800 hour, cloudy and windy from 0800 to 1300 hours, then light rain occurred until a thunderstorm at 1700 hours that lasted until dark
11 March	0603	1751	11.1	-1.7	Light rain occurred before 1100 hours, then cloudy skies until dark
12 March	0602	1751	11.7	-1.7	Sunny and calm
22 May	0542	1950	29.5	17.2	A 2-hour rain began at 1230 hours, remaining periods were sunny
23 May	0541	1951	30.1	17.2	Sunny
18 July	0546	1958	36.1	22.2	Hazy
19 July	0547	1958	36.1	22.2	Sunny and clear
15 August	0602	1933	36.7	20.0	Sunny
16 August	0603	1932	36.7	20.6	Sunny with occasional partly-cloudy conditions
17 October	0653	1810	23.9	12.2	Cloudy during morning periods; remaining periods were sunny
18 October	0654	1809	23.9	9.4	Cloudy during morning periods; remaining periods were sunny

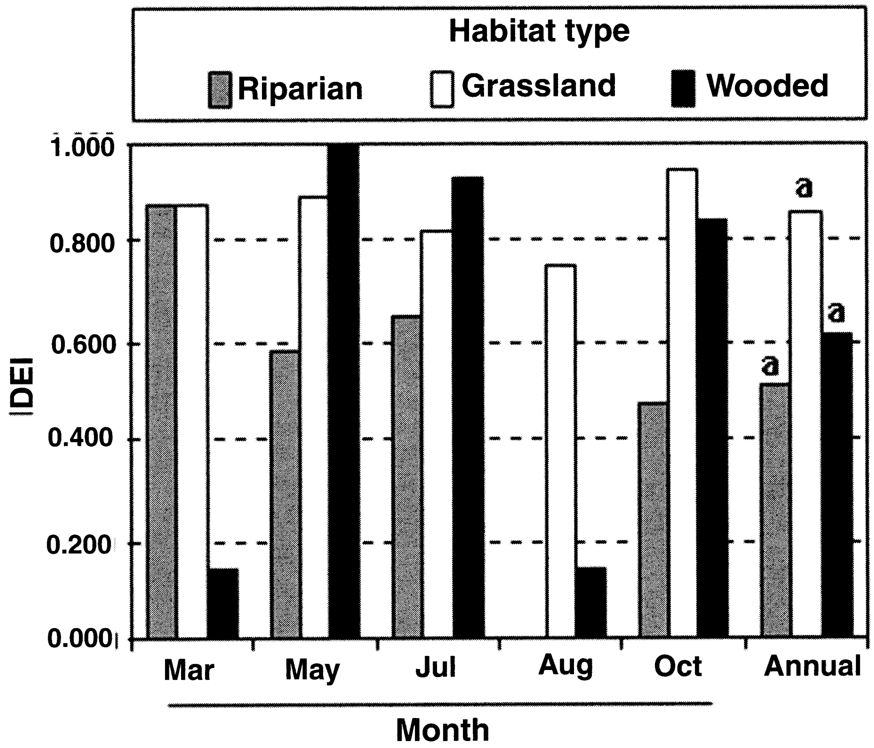

Fig. 3. Monthly and annual comparison of cattle distribution eveness indicated by the DEI (Distribution Evenness Index) for different habitat types in the studied landscape, Glendale Farms, north-central Ala. Annual means with the same letter indicate no significant difference (P < 0.05).

Because the indices themselves will be normally distributed if the Shannon-Wiener index is calculated for a number of samples (Taylor 1978), it is possible to use parametric statistics to compare sets of DEI values (Magurran 1988). To test the sensitivity of the DEI to specific cattle behaviors, the paired t-test ($P < 0.05$) was performed (PROC MEANS, SAS® version 6.12) to test differences between the DEI values for total activities and grazing activities at different time intervals in the grassland habitat and grazing activities in the grassland habitat at different zone-subdivision levels. Analysis of variance (PROC ANOVA, SAS® version 6.12) and the least significant difference ($P < 0.05$) were used to detect overall differences for total activities in different landscape habitat types, and for grazing activities in the grassland habitat at different daytime periods.

Results and Discussion

Location choice distribution

Consistently high cattle distribution evenness was indicated for the grassland habitat throughout this study. Higher distribution evenness was detected in the riparian habitat during March compared to May, July, and October (Fig. 3). However, extremely uneven use of the riparian habitat by cattle was noted in August since evenness equaled 0 at that time. The wooded habitats had very high DEI values in May, July, and October, and very low Distribution Evenness Index (DEI) values in March and August. Annual means of diurnal observations indicated that evenness of cattle distribution was low in riparian and wooded habitats, and high in the grassland habitat. About 90% of total activities that occurred in the grassland habitat were grazing and about 75% of the total activities that occurred in wooded or riparian habitats were lying and loafing (Zuo 2001). Thus grazing activities caused consistently higher distribution evenness in the grassland habitat while unstable evenness patterns in riparian or wooded habitats were most closely related to seasonal effects on loafing and lying activities.

Effects of temporal and spatial levels

Higher evenness of cattle distribution in the grassland habitat was indicated by the DEI calculated using 15-min interval observation records for both location choice and grazing activities during the cool-season versus the warm-season (Table 2). The most uneven distribution occurred in August, the warmest period during this study, when cattle spent the majority of diurnal time lying or loafing in wooded habitats and their foraging activities occurred mainly in shaded areas of the grassland habitat close to wooded or shaded riparian habitats. The similar evenness pattern of total activities and grazing activities demonstrated the major influence of grazing activities on cattle location choice in the grassland habitat (Table 2). On the other hand, this similarity further indicated that cattle spent the majority of time in the grassland habitat for grazing activities.

No significant difference was detected between the DEI values calculated using 30-min interval records and those based on 15-min interval observation records (Table 2). However, the DEI values calculated using 60-min interval records were

Table 2. Comparison of DEI (Distribution Evenness Index) values for cattle location choice for all activities and grazing activity in the grassland habitat at different time-interval levels, Glendale Farms, north-central Alabama 2000.

	All activities			Grazing activity		
	15-min	30-min	60-min	15-min	30-min	60-min
March[†]	0.883	0.890	0.865	0.868	0.873	0.846
May	0.896	0.820	0.730	0.903	0.840	0.720
July	0.822	0.820	0.750	0.823	0.830	0.730
August	0.756	0.780	0.680	0.749	0.780	0.690
October	0.944	0.930	0.840	0.934	0.930	0.840
	Paired t-test					
	15-min vs. 30-min	15-min vs 60-min	30-min vs. 60-min	15-min vs. 30-min	15-min vs. 60-min	30-min vs. 60-min
Difference (probability)	0.012 (0.5153)	0.087 (0.0225)*	0.075 (0.0050)*	0.005 (0.7745)	0.090 (0.0278)*	0.085 (0.0054)*

[†]October through April = cool season; May through September = warm season.
*Indicates significant difference at $P < 0.05$.

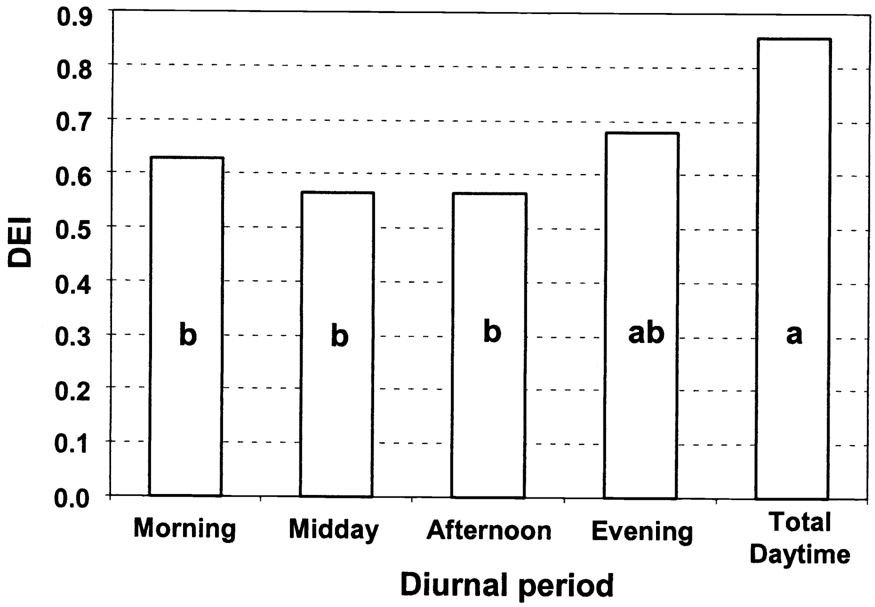

Fig. 4. Grazing distribution evenness in the grassland habitat indicated by the mean DEI (Distribution Evenness Index) for different diurnal periods, March to October 2000, Glendale Farms, north-central Ala. Means with different letters indicate a significant difference ($P < 0.05$).

consistently and significantly lower than the DEI values based on 15-min or 30-min interval records. This decrease indicated that information about actual cattle distribution patterns in this study could have been lost if the observation interval had been greater than 30 min.

Relative stability of the DEI was detected at various levels of grassland habitat subdivision for both 15- and 30-min interval records, especially during the cool-season (Table 3). Higher DEI values were obtained during the warm season when the 6- or 9-zone subdivision was used for the grassland habitat; an exception was the 6-zone subdivision in August. It appeared that subdivision with a larger zone size inflated the unevenness of cattle distribution when the true value of DEI was actually relatively low. On the other hand, the subdivision of a given habitat area itself should not be so small as to impact animal aggregation behavior, namely, each zone should be able to hold all animals together with enough inter-animal distance, about 78.5 m^2 $head^{-1}$ (Phillips 1993). For example, the 18-zone grassland habitat subdivision in this study allowed approximately 80 m^2 $head^{-1}$ when all cattle were in 1 zone, even during the cool-season when a higher stocking density was employed.

Table 3. Comparison of DEI (Distribution Evenness Index) values for 15- and 30-min interval records at different levels of grassland habitat subdivision, Glendale Farms, north-central Ala., 2000.

	15-min interval records			30-min interval records		
	18-zone	9-zone	6-zone	18-zone	9-zone	6-zone
March†	0.868	0.865	0.881	0.875	0.886	0.900
May	0.903	0.968	0.991	0.843	0.899	0.949
July	0.823	0.880	0.892	0.839	0.899	0.878
August	0.749	0.769	0.644	0.788	0.818	0.719
October	0.934	0.965	0.985	0.930	0.961	0.987
			Paired t-test			
	18-zone vs. 9-zone	18-zone vs 6-zone	9-zone vs. 6-zone	18-zone vs. 9-zone	18-zone vs. 6-zone	9-zone vs. 6-zone
Difference	–0.034	–0.023	–0.011	–0.038	–0.032	0.006
(probability)	(0.0515)	(0.5365)	(0.7250)	(0.0144)*	(0.3317)	(0.8283)

†October through April = cool season; May through September = warm season.

Temporal distribution of grazing activities

Consistently high evenness of diurnal grazing patterns in the grassland habitat was indicated by the DEI based on total daytime observations, although uneven grazing patterns were detected for different daytime periods from March to October (Fig. 4). This result suggested that cattle could choose different zones at different times with small overlap between them, or their patch preference at different periods of daytime was complementary across the total daytime period. This temporal distribution pattern of cattle grazing activities supports the suggestion made by Senft et al. (1987) that observed distribution patterns are the cumulative effects of diet selection and feeding station behaviors. It also supports the conclusion made by Bailey (1995) that no patch preferences will be measured in a homogeneous area if data are pooled within a day, and time spent in patches is not consistent throughout the day.

Advantages and drawbacks

An important criticism of grazing behavior studies has been that there is no standardized technique of observation (Bailey et al. 1996), thus making comparison of animal behavioral patterns difficult between different studies. The use of the DEI in this study demonstrated that the index has relative stability for observation intervals less than 30-min and different grassland habitat subdivision levels. We hypothesize that the relevant sensitivity or stability range of DEI could be acquired for larger landscape areas based on livestock activities pooled across several weeks. This information could then be used to describe overall grazing patterns in the landscape as well as evenness of forage utilization. In these circumstances, Global Positioning System (GPS) technology could be used to obtain animal landscape positions at 5-min intervals (Turner et al. 2000). Thus, additional information about livestock distribution could be obtained for larger landscapes through combination of the DEI with GPS technology.

The DEI appears to be a relatively simple and direct method of obtaining information about uniformity of cattle distribution in heterogeneous landscapes. The advantages of temporal and spatial stability should facilitate use of the DEI for rapid evaluation of the effects of certain management practices on cattle distribution patterns for the same pasture, or comparison between different studies with similar spatial and temporal scales.

Summary and Conclusions

Uniformity of cattle distribution patterns in a grazed landscape was described by a Distribution Evenness Index (DEI) based on modification of the Shannon-Wiener index. The DEI also provided general information about evenness of cattle habitat use for various behaviors within the heterogeneous landscape studied. When the DEI was calculated based on observations at a given time interval, cattle distribution evenness could be described for any behavior type or temporal period. This study, conducted at a small spatial scale (3–4 ha), indicated that observations should be made at time intervals of 30-min or less since behavioral information was lost when longer intervals were used. However, relative stability of the DEI calculated between selected spatial and temporal scales in this study indicated that comparison of the evenness of livestock habitat use and grazing patterns between different studies at similar spatial and temporal scales is possible and should be explored through further research.

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56: 152-158 March 2003

Hydrologic and sediment responses to vegetation and soil disturbances

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Abstract

Soil erosion has been linked to stream sedimentation, ecosystem degradation, and loss of rangeland productivity. However, knowledge of soil loss, as it affects rangeland productivity or ecosystem sustainability is lacking. We evaluated the effects of 3 levels of vegetation cover reduction (0, 27%, and 43%) and soil removal (0, 12, and 24 tonnes ha^{-1}) on soil surface runoff and sediment yield in a sagebrush [*Artemisia tridentata* var. *vasseyana* (Rydb.) Beetle] steppe under simulated rainfall. Time to runoff initiation was affected by the vegetation cover reduction treatments, but not by the soil removal treatments. The 43% vegetation canopy reduction treatment resulted in a shorter time to runoff initiation than did the 27% and 0% canopy reduction treatments (p = 0.002). Results from analysis of covariance indicated that vegetation reduction and soil removal did not significantly affect sediment yield or runoff quantities in the first year following treatments. Multiple regression analysis revealed total sediment yield was related to forb cover, sand in the upper soil profile (0-5 cm), and the amount of bare ground. Time to runoff initiation was positively correlated with slope. Despite the lack of significant treatment differences, we do not conclude that these soil removal and vegetation reduction treatments had no affect on soil surface hydrology and sediment yield. There are numerous studies that show a strong relationship between vegetation reduction and soil erosion. Future research at this site may reveal long-term treatment effects that were not apparent in first year results.

Key Words: rainfall simulation, erosion, runoff, hydrology, sagebrush steppe

Resumen

La erosión del suelo ha sido vinculada a la sedimentación de las corrientes de agua, la degradación de ecosistemas y la perdida de productividad de pastizales. Sin embargo, se carece de conocimiento de como la perdida de suelo afecta la productividad de los pastizales o la sostenibilidad del ecosistema. Evaluamos el efecto de 3 niveles de reducción de cobertura vegetal (0, 27 y 43%) y remoción de suelo (0, 12 y 24 ton ha^{-1}) en el escurrimiento superficial y la producción de sedimento en una estepa de "Sagebrush" [*Artemisia tridentata* var. *vasseyana* (Rydb.) Beetle] bajo lluvia simulada. El tiempo de inicio del escurrimiento superficial fue afectado por los tratamientos de reducción de cobertura vegetal, pero no por los de remoción de suelo. El tratamiento de 43% de reducción de cobertura vegetal resultó en un menor tiempo de iniciación del escurrimiento que el obtenido por los tratamientos de reducción de cobertura de 0 y 27% (P = 0.002). Los resultados del análisis de covarianza indicaron que la reducción de la vegetación y la remoción del suelo no afectaron significativamente el rendimiento de sedimento o las cantidades escurrimiento en el primer año después de aplicados los tratamientos. El análisis de regresión múltiple reveló que la producción total de sedimento estuvo relacionada a la cobertura de hierbas, contenido de arena en el perfil superior del suelo (0—5 cm) y la cantidad de suelo desnudo. El tiempo de inicio del escurrimiento estuvo positivamente correlacionado con la pendiente. A pesar de la falta de diferencia significativa entre tratamientos nosotros no concluimos que estos tratamientos de remoción de suelo y reducción de vegetación no tuvieron efecto en la hidrología superficial del suelo y la producción de sedimento. Hay numerosos estudios que muestran una fuerte relación entre la reducción de vegetación y la erosión del suelo. Futuras investigaciones en este sitio pueden revelar efectos a largo plazo de los tratamientos que no fueron aparentes en los resultados del primer año.

Soil erosion is a major problem throughout the world (Meyers 1984, Pimentel et al. 1995) and has been recognized as a problem in the United States since the early 1900's (Sampson 1918). In the United States, an estimated 4.4 billion tonnes of soil are eroded by wind and water every year (Bills and Heimlich 1984). In many cases, these soil losses lead to increased sediment loads in streams and rivers which can reduce productivity of aquatic ecosystems, shorten the life span of ponds and reservoirs (Buckhouse and Gaither 1982), and impair fish habitat (Binkley and Brown 1993). In addition to ecological impacts, soil erosion can lead to decreased rangeland productivity through the loss of organic matter and plant nutrients. A principle challenge for rangeland managers is to optimize forage production for herbivores without reducing the ecological integrity of rangelands or decreasing their societal benefits.

Not all erosion is a result of land mismanagement. Soil erosion is a natural process of dislodgment of soil particles from the surface and subsequent transport by water and wind (Brooks et al.

This research was funded by the United States Department of Agriculture, Agricultural Research Service and the Colorado State University Agricultural Experiment Station. The authors wish to thank the Arapaho National Wildlife Refuge and all the support personnel for their assistance on the study.

Manuscript accepted 22 May 02.

1997). Erosion at a rate greater than 11.2 tonnes ha^{-1} yr^{-1} exceeds the estimated rate at which most parent material weathers (McCormack and Young 1981). Accelerated erosion and changes in soil surface hydrology have been reported under conditions of reduced vegetation cover and altered soil structure (Sampson 1918, McCalla et al. 1984, Linse et al. 2001). Preventing accelerated soil erosion has been regarded as the key to maintaining rangeland ecosystem sustainability (Buckhouse and Gaither 1982). Land managers, however, do not have scientifically based evidence for the amount of vegetation cover necessary to maintain rangeland sustainability. The influence of soil surface degradation (i.e., removal of the soil "A" horizon, changes in surface roughness, decreasing micro-channel sinuosity, soil compaction and previous soil erosion) on rangeland sustainability is even less understood.

To prevent soil erosion by water, it is necessary to maintain the soil surface in a condition that readily accepts water (Brooks et al. 1997). The soil "A" horizon often contains significant amounts of organic matter which improves infiltration and increases soil water holding capacity. Therefore, removal of the "A" horizon can lead to increased erosion of underlying soil horizons (Pimentel et al. 1995). The effects of soil removal on soil surface hydrology and sediment yield from rangelands are not well understood and must be clarified before accurate soil loss thresholds are developed.

The purpose of this research project was to determine the effects of vegetation cover reduction and soil removal on soil surface hydrology and sediment yield in a big sagebrush [*Artemisia tridentata* var. *vasseyana* (Rydb.) Beetle] steppe ecosystem. The main hypotheses of this project were that (1) a 27% reduction in vegetation cover would not result in altered soil hydrology, (2) a 43% reduction in cover would result in increased runoff and sediment production, (3) soil removal of 12 tonnes ha^{-1} would not affect soil surface hydrology, and (4) soil removal of 24 tonnes ha^{-1} would result in increased runoff and sediment yield.

Methods and Materials

Site Description

Field experiments were conducted on an upland area of the Arapaho National Wildlife Refuge (ANWR), 15 km south of Walden, Colo. The ANWR is located in an intermountain glacial basin known as North Park and encompasses 10,037 hectares. The study site (40° 36' 48.5"N, 106° 16' 29.6"W) was grazed by livestock prior to being designated as a wildlife refuge in 1967 (Lanier 1999) and is representative of a sagebrush steppe ecosystem classified in good rangeland health. Current management of the research site is exclusion of livestock grazing, but includes winter grazing by 200–500 free-roaming Rocky Mountain Elk (*Cervus elaphus canadensis*, Erxleben).

The site is at an elevation of approximately 2,500 m, receives an average annual precipitation of 240 mm, and experiences an average of 30 consecutive frost-free days per year. Soils are listed as a cabin sandy loam in the subgroup Argic Cryoboroll. These soils are deep, well drained soils that formed in gravelly alluvium, and are underlain by gravelly sand at a depth of 50 to 100 cm (USDA 1981). The average soil texture was 61% sand, 22% silt, and 17% clay, but ranged from 55–64% sand, 19–27% silt, and 14–25% clay.

Experimental Design

The experimental design was a randomized complete block experiment with a 3 x 3 factorial arrangement of treatments. The treatments consisted of 3 levels of soil removal (0, 12, and 24 tonnes ha^{-1}) and 3 levels of plant canopy reduction (0, 27, and 43%) with 3 replications of each treatment (27 plots). Individual treatments were randomly assigned to pairs of plots. Each plot was paired with an adjacent plot of the same size according to similar vegetation characteristics and amount of bare ground. One of the plot pairs was used for destructive sampling (above ground biomass and soil bulk density) and the other plot was used for collecting sediment yield and runoff variables. The plots were located on a 7% slope within an exclosure area of approximately 5,000 m^2.

Plot Installation and Rainfall Simulator

Plots measuring 2 x 0.6 m were delineated by inserting 15 cm wide metal sheets into the soil to a depth of 3–6 cm on the up-slope end and sides of each plot. Plot pairs, separated by one meter, were oriented lengthwise with the slope. Runoff collection troughs were placed at the down-slope end of each plot and sealed against the soil surface with an expanding foam. Rainfall simulations took place during the period from 27 July 1999 to 5 August 1999. A rotating boom rainfall simulator developed by the University of Wyoming (Linse 1992) was used to apply simulated rainfall to plots at an intensity of 100 mm $hour^{-1}$ for 30 minutes (dry run) at antecedent soil moisture. After 30 minutes, the third of 3 spray nozzles was activated and water pressure was increased to apply rainfall at an intensity of 150 mm $hour^{-1}$ for an additional 30 minutes (wet run).

The rainfall intensity of 100 mm $hour^{-1}$ was chosen to simulate a high intensity-low frequency storm that would exceed the infiltration capacity and produce measurable runoff (Linse et al. 2001). The increased application rate, in the wet run, was used to determine whether sediment yield from this ecosystem was energy limited. Six wedge rain gauges were spaced at equal distances around the perimeter of each plot to measure the total amount of simulated rainfall that reached the plot during the dry and wet runs. Runoff samples were manually collected every 2 minutes, for a duration of 6 seconds, from each plot.

Treatments

Soil and vegetation treatments were applied in July 1999. Soil was vacuumed from plot surfaces using a gas-powered blo-vac. Soil was vacuumed from bare ground, coppice dunes, and through the crowns of all forb and grass plants to achieve a uniform soil removal. Vacuumed soil was field weighed and taken back to the lab to dry, obtain a more accurate weight, and determine particle size. Non-woody canopy cover was killed by spraying Roundup herbicide through one of 2 perforated board templates onto circular patch areas within the plots. The exposed area of template 1 represented 30% of the plot area. The exposed area of template 2 represented 60% of the plot area. However, vegetation cover reduction from these treatments averaged 27% and 43% for the 30% and 60% templates, respectively. Where shrub cover was exposed beneath the perforations, the shrub canopy was spray painted and removed with pruning shears. The resulting soil-vegetation characteristics were designed to represent variations in degraded rangeland sites.

Plot Characterization

Vegetation cover and soil surface roughness were measured before and after treatments were applied. Vegetation cover was estimated by individual species using the point frame method (Bonham 1989, Linse et al. 2001). A 2 x 0.6 m 100 point horizontal plane pin table was placed onto each plot and pins were lowered until either vegetation, standing litter, rock, surface litter or bare ground was intercepted. The initial pin hit was used to determine canopy cover by species. As many as 2 pin hits were recorded to determine canopy cover of sagebrush and under story herbaceous species cover. Each pin was then lowered to the soil surface to characterize soil surface cover. Absolute canopy cover by species and absolute soil surface cover was recorded as the percentage of total pin strikes for that cover class per total pin strikes for the plot. Cover, by plant life form, and soil surface characteristics were categorized into 8 classes: grasses (by species), forbs (by species), shrubs (by species), standing litter (current year litter which had not fallen to the ground and standing woody debris), cryptograms, bare ground, rock, and litter. Surface roughness was measured using a digital caliper resting on top of the lowered pins. Surface roughness was calculated as the standard deviation of the elevation of 100 pins (Kuipers 1957, Linse et al. 2001). Finally, the hill slope (%) was calculated by determining the regression equation for the average slope of a plane of the plot as determined by pin height measurements.

In each destructively sampled plot, two, 192 cm^3 soil samples were collected to a depth of 10 cm. These samples were divided into 2 subsamples at 0–5 cm and 5–10 cm to determine soil bulk density using the core method (Blake and Hartge 1986) and soil texture according to the hydrometer method (Bouyoucos 1962). Immediately prior to each rainfall simulation, three, 51 cm^3 soil cores were removed adjacent to the plot pair. These samples were divided into subsamples at 0–5 cm and 5–10 cm to determine antecedent soil moisture using the gravimetric method (Gardner 1986).

Runoff Hydrograph

Hydrographs were generated by plotting runoff values over time for dry and wet runs. The shape of the hydrograph was used to evaluate the time to runoff initiation, equilibrium runoff rate, and equilibrium runoff ratio (Frasier et al. 1998a). Time to runoff initiation was defined as the time when the runoff rate exceeded 5% of the rainfall rate. The equilibrium runoff period was defined as the time when the rising limb of the hydrograph leveled off until the end of the appropriate time period (dry or wet run). The equilibrium runoff ratio was defined as the average percentage of applied rainfall that was collected as runoff during the equilibrium runoff period and was calculated for the dry and wet runs.

Sedigraph

Every runoff sample was transferred to an individual sediment bottle until peak runoff was reached (determined as the point at which runoff leveled off or showed an initial decline). After the initial peak runoff rate was attained, every other runoff sample was transferred to a sediment bottle for subsequent sediment analysis. Prior to sediment filtration, paper filters with 1 micrometer pores were dried at 40° C for 4 hours and weighed. Sediment samples were gravity filtered and then dried for 6 hours at 80° C and weighed (Gutierrez-Castillo 1994). A sedigraph was generated by plotting sediment yield vs. time. The area under the curve of this graph was integrated to determine total sediment yield. Sediment yield is reported in kg ha^{-1} mm $runoff^{-1}$. These units adjust sediment yield for the amount of runoff carrying the sediment to the trough. In addition to these parameters, sediment yield which occurred between the time to runoff initiation and the end of the dry run was subdivided into 3 periods (early, middle, and late).

Data Analysis

Data were analyzed using standard statistical programs (SAS Institute Inc. 1998) available for analysis of covariance (PROC GLM), multiple regression analysis (PROC REG), and repeated measures analysis of variance (PROC MIXED). Differences were considered significant at $P < 0.10$. Analysis of covariance was used to determine whether soil removal or vegetation reduction significantly affected runoff or sediment yield. Covariates included slope, antecedent soil moisture, soil bulk density, total live vegetation cover, sagebrush cover, litter cover, grass cover, forb cover, bare ground, soil texture, and surface roughness. Multiple linear regression, with stepwise selection, was used to determine whether significant relationships existed between independent variables (bare ground, grass cover, sagebrush cover, litter cover, total vegetation cover, sand, slope, soil bulk density, antecedent soil moisture, surface roughness, and rainfall intensity), and sediment yield or runoff values (SAS Institute Inc. 1998). The average sediment yield in each period was used in repeated measures analysis of variance to determine whether there was a significant decrease in sediment yield over time. Analysis of sediment yield residual plots indicated the need for a natural logarithm (ln) transformation of these data. Therefore, all data in this study were analyzed using a ln transformation. This transformation was also used by Sharpley (1985) to analyze sediment yield.

Results and Discussion

Vegetation and Soil Parameters

Average pre-treatment vegetation canopy cover across all plots was 45%, but ranged from 30 to 65%. Average soil bulk density across plots was 1.22 g cm^{-3} in the upper 0–5 cm and 1.25 g cm^{-3} in the lower 5-10 cm of the soil profile. Soil bulk density was not significantly different among treatments.

Water erosion typically removes fines (clay- and silt-sized soil particles) and leaves coarse particles behind (Ellison 1944, 1948, Pearce et al. 1998). Although particles larger than clay and silt, and large soil aggregates, may be detached by raindrop splash, they settle out of the overland flow much sooner than finer particles (Ellison 1944, Pearce et al. 1998). The soil texture of the vacuumed soil was 65% sand, 22% silt and 13% clay, with ranges of 64–69%, 19–24%, and 12–15%, respectively. This texture was not statistically different from the in situ soil texture. This suggests that vacuuming of the surface soil did not selectively remove silt- and clay-sized particles, as would be expected under natural water erosion events. Although soil particle size was not affected by the vacuuming, the soil removal treatment did affect surface roughness. The average surface roughness of vacuumed plots (27 S.D.) was significantly greater ($P < 0.001$) than the average pretreatment surface roughness (22 S.D.).

Runoff

The amount of runoff is the difference between the amount of water applied minus the water retained on the soil and plant surfaces, and the amount that infiltrated into the soil (Frasier et al. 1998a). Three runoff parameters were analyzed: time to runoff initiation, equilibrium runoff ratio in the first 30 minutes (dry run) of the rainfall simulation, and equilibrium runoff ratio in the last 30 minutes (wet run) (Table 1).

In many rangeland situations, the runoff characteristics at the beginning of the storm, such as time to runoff initiation, are most important because storm durations are too short to develop equilibrium runoff

Table 1. Means (standard errors) for runoff parameters by treatment from sagebrush steppe rainfall simulation plots. Treatment differences were not significant at P < 0.10.

Soil Removal	Vegetation Reduction	Time to Runoff Initiation	Equil. Runoff Ratio for Dry Run	Equil. Runoff Ratio for Wet Run
(tonnes ha^{-1})	(%)	(minutes)	(%)	(%)
0	0	8.3 (2.7)	34 (8.7)	59 (7.5)
0	27	2.3 (0.7)	48 (8.7)	68 (13.3)
0	43	4.3 (1.3)	45 (13.9)	67 (9.8)
12	0	5.7 (1.3)	43 (8.7)	71 (13.9)
12	27	3.7 (0.7)	45 (11.0)	65 (6.9)
12	43	4.3 (1.8)	47 (9.8)	64 (8.7)
24	0	6.3 (2.9)	50 (11.5)	78 (9.8)
24	27	3.0 (1.2)	43 (9.2)	69 (9.8)
24	43	5.7 (1.8)	30 (6.4)	63 (2.3)

(Frasier et al. 1998a). Our results showed that time to runoff initiation was affected by the vegetation canopy reduction treatments, but not by the soil removal treatments. The 43% vegetation canopy reduction treatment resulted in a shorter time to runoff initiation than did the 27% and 0% canopy reduction treatments (P = 0.002). Nyhan et al. (1984) and Giordanengo (2001) found that antecedent soil moisture had a pronounced effect on time to runoff initiation. However, their results were from consecutive rainfall simulations that occurred over successively wet conditions on the same plots. In this study, antecedent soil moisture did not vary great enough from plot to plot to affect runoff variables.

Equilibrium runoff rates have been used as indicators of treatment differences in previous rainfall simulation studies (Simanton et al. 1991, Frasier et al. 1998b). Equilibrium runoff occurs when soil surface layers are saturated and is representative of long duration precipitation events that exceed the infiltration rate (Frasier et al. 1998b). Because equilibrium runoff rates are influenced by rainfall intensity, we used equilibrium runoff ratios [(runoff rate divided by rainfall rate) x 100] to compare treatment effects. Equilibrium runoff ratios in the dry and wet runs were not significantly affected by treatments (P = 0.732 and 0.872, respectively). These results support findings by Busby and Gifford (1981), who reported that removal of vegetation did not have an immediate effect on infiltration.

Because the herbicide-treated dead vegetation cover was not removed prior to rainfall simulations, the standing litter that remained was likely affecting rainfall interception in the same manner as live vegetation. In addition, the vegetation treatments most likely did not have an affect on channel formation. Although not measured, it can be expected that over time, that regrowth of vegetation in the herbicide-treated areas may help to maintain the degree of channel formation present at the time of rainfall simulations. Unless annual treatments are applied, the desired degraded rangeland conditions may not be maintained, and it is unlikely that long term effects from these vegetation treatments will be noticeable.

Past research has shown that amount of slope (Wischmeier and Smith 1978, Sharpley 1985) and bare ground (Branson and Owen 1970, Wischmeier and Smith 1978) were positively correlated with runoff. However, our results indicated that slope and bare ground were not significant covariates and did little to explain treatment differences in runoff data. Other covariates that were used, but did not significantly affect equilibrium runoff ratios, included total live vegetation cover, sagebrush cover, grass cover, litter cover, surface roughness, antecedent soil moisture, and soil bulk density. Soil bulk density only represented bare interspace areas and did not vary significantly enough among treatments to influence runoff. The absolute cover of vegetation may not be as important a covariate as the spatial distribution of the vegetation over the plot. The spatial distribution of vegetation influences the microchannel network which, in turn, may have dominated the runoff processes in this study.

The equilibrium runoff ratio, averaging all treatments, was significantly greater (P < 0.0001) in the wet run (67%) than in the dry run (43%). In addition to the increase in rainfall intensity, surface sealing of these soils may account for the increased runoff ratio (Farres 1978). Also, saturation of surface litter, plant surfaces and soil macropores would result in an increased proportion of rainfall reaching the soil surface and a decrease in infiltration.

Sediment Yield

There was an interaction between soil and vegetation treatments (P = 0.096) for total sediment yield. A 27% vegetation reduction resulted in greater sediment yield, at the soil removal level of 0 tonnes ha^{-1}, than did a 0 or 43% vegetation reduction. Analyses of sediment data were done by soil treatment, averaging over vegetation treatment, and visa versa. Four sediment yield parameters were analyzed: total sediment yield over the 60 min rainfall simulation, sediment yield over the first 10 min, sediment yield for the dry run, and sediment yield for the wet run (Table 2).

Analysis of covariance indicated that total sediment yield was not significantly affected (P = 0.441) by soil or vegetation treatments. Likewise, sediment yield in the first 10 minutes (P = 0.469), first 30 minutes (P = 0.624), and last 30 minutes (P = 0.229) after rainfall simulations began was not significantly affected by soil or vegetation treatments. Given the slow decomposition rates in this arid environment, the roots and shoots of herbicide-treated plants should have been intact when the rainfall simulations occurred. Therefore, the indirect effects of vegetation on sedi-

Table 2. Means (standard errors) for sediment yield parameters by treatment from sagebrush steppe rainfall simulation plots. Treatment differences were not significant at P < 0.10.

Soil Removal	Vegetation Reduction	Sediment Yield Total	1st 10 Minutes	Dry Run	Wet Run
(tonnes ha^{-1})	(%)	--------------------(kg ha^{-1} mm $runoff^{-1}$)			----------------------
0	0	761 (429)	218 (111)	461 (234)	300 (217)
0	27	4506 (2823)	1124 (572)	2439 (1420)	2067 (1404)
0	43	685 (332)	256 (135)	434 (218)	244 (122)
12	0	836 (77)	222 (48)	443 (37)	393 (114)
12	27	999 (167)	235 (80)	601 (176)	397 (44)
12	43	1502 (616)	323 (165)	632 (285)	871 (422)
24	0	2178 (1776)	250 (206)	1108 (974)	1070 (804)
24	27	504 (97)	150 (44)	253 (83)	250 (57)
24	43	1164 (456)	335 (113)	665 (263)	499 (232)

ment yield (i.e., increased litter cover, reduced bulk density and increased infiltrability), reported by Wilcox et al. (1988), was probably operating during rainfall simulations. In fact, our results indicated that an instantaneous reduction of live vegetation cover did not significantly affect runoff or sediment yield. Research by Busby and Gifford (1981) and Wilcox et al. (1988) has also shown that vegetation removal does not immediately affect infiltration or runoff. Similarly, Johnson and Gordon (1988) reported that sagebrush canopy removal did not significantly affect soil loss. If rainfall interception, infiltration, runoff and channel sinuosity are not being affected by vegetation treatments, then sediment yield will most likely not be altered. A more drastic change in vegetation cover, not just an aboveground kill, is likely necessary to influence sediment yield.

The effect of soil removal on subsequent sediment yield is not well documented. Results of this study did not support the hypothesis that soil removal of 24 tonnes ha^{-1} would result in increased sediment yield. One possible explanation is that the significant increase in surface roughness created by the soil vacuuming reduced sediment movement down slope. However, Linse et al. (2001) reported a weak correlation between surface roughness and sediment yield. The spatial variability of surface roughness, as opposed to an absolute value, may be a more accurate predictor of sediment yield. Linse (1992) explained how the spatial variability of surface roughness can affect sediment yield. If surface roughness is greater at the bottom of the plot, it may act to trap sediment from the top of the plot, whereas surface roughness concentrated at the upslope end of the plot will not trap as much sediment before it reaches the collection trough. Also, if surface roughness is interconnected along one side of the plot, the depressions may join to form a microchannel or rill. This may allow for considerable erosion from the plot. Using the point-frame method to measure surface roughness, it is possible to describe the spatial variability of surface roughness, but without quantifying the spatial arrangement of vegetation within the topography (e.g., degree of channel formation). Such an analysis is incomplete.

Sediment yield in runoff water generally decreases over time during a rainfall event (Ellison 1944, Gutierrez-Castillo 1994). Contrary to their findings, results from the repeated measures analysis of variance in this study revealed an increase in sediment yield over time ($P < 0.001$). Sediment yield in the late period was significantly greater than in the early period ($P < 0.001$) and the middle period ($P = 0.024$). This may be an indication that soil erosion in this sagebrush steppe is not a source-limited process. As such, removal of 24 tonnes ha^{-1} may not be drastic enough to affect subsequent sediment yield. This may help to explain the absence of significant differences in sediment yield among the soil removal treatments.

Predicting Runoff and Sediment Yield

Runoff

Three runoff parameters were analyzed: time to runoff initiation, equilibrium runoff ratio in the dry run, and equilibrium runoff ratio in the wet run. Independent variables included total vegetation cover (%), forb cover (%), grass cover (%), sagebrush cover (%), litter cover (%), bare ground (%), rainfall intensity (mm/hr), slope (%), surface roughness (SD), sand in the upper 5 cm of the soil profile (%), and soil bulk density (g/cm^3). Results of the multiple regression analysis indicated that time to runoff initiation was positively correlated with slope ($R^2 = 0.39$, $P = 0.005$, Table 3). Other researchers (Flenniken 1999) have reported a correlation between time to runoff initiation and rainfall intensity. In our study, rainfall intensity was not correlated with time to runoff initiation, but did show a positive correlation with the dry run equilibrium runoff ratio ($R^2 = 0.34$, $P = 0.002$). Equilibrium runoff ratio in the wet run was not correlated with any of the independent variables used in the multiple regression analysis. Variables such as the spatial distribution of microtopography, channel sinuosity, and average infiltrability for each plot may be controlling runoff to a greater degree than the independent variables used in this analysis.

Sediment Yield

Many researchers (Meeuwig 1969, McCalla et al. 1984 and Linse et al. 2001) have documented changes in sediment yield with changes in litter cover, vegetation cover, bare ground, and surface roughness. In our study, total sediment yield was negatively correlated with forb cover ($P = 0.018$) and the amount of sand in the upper 5 cm of the soil profile ($P = 0.016$), and positively correlated with bare ground ($P = 0.055$) for a model R^2 of 0.60 (Table 3). Sediment yield in the first 10 minutes also showed a negative correlation with forb cover ($P = 0.011$) and sand in the upper 5 cm of the soil profile ($P = 0.014$), for a model R^2 of 0.56. The negative correlation between sand in the upper 5 cm of the soil profile and sediment yield may be attributed to the fact that sandier soils experience higher infiltration rates which results in a lower volume of overland flow. This lower overland flow provides a lower capacity for carrying soil particles and lower energy for dislodging soil particles as it moves down slope. In addition, sand particles are more difficult to transport down slope compared to finer grained particles such as silt or clay.

Bare ground was not strongly correlated with any of the sediment yield parameters analyzed (e.g., partial R^2 values were 0.13 and 0.14 for total sediment yield and sediment yield in the wet run, respectively). Branson and Owen (1970) also reported a low correlation between bare ground and sediment yield (R^2 of 0.03 to 0.24). Some researchers, however, have reported highly positive correlations between bare ground and sediment yield (Hofmann et al. 1983). The lack of correlation in this study may have resulted from differences in the

Table 3. Results of stepwise multiple regression analysis for sediment and runoff variables from sagebrush steppe rainfall simulation plots.

	Partial R^2 Values for Independent Variables					
Dependent Variables	Slope	Forb Cover	Sand (0-5 cm)	Bare Ground	Rainfall Intensity	Model R^2
	(%)	(%)	(%)	(%)	($mm\ hr^{-1}$)	
Sediment ($kg\ ha^{-1}\ mm\ runoff^{-1}$)						
Total	—	0.15	0.32	0.13	—	0.60
First 10 min	—	0.34	0.22	—	—	0.56
First 30 min	—	—	0.29	—	—	0.29
Second 30 min	—	0.11	0.31	0.14	0.11	0.67
Runoff						
Time to runoff (min)	0.39	—	—	—	—	0.39
Equil. Runoff Ratio (dry run)	—	—	—	—	0.34	0.34
Equil. Runoff Ratio (wet run)	—	—	—	—	—	—

spatial distribution of bare ground from plot to plot. If bare ground dominates the lower portion of the plot, significant channeling may form throughout the rainfall simulation, allowing high sediment yields to occur. However, if bare ground is randomly distributed in small patches across the plot, then significant sediment yield will be unlikely given the lack of connectivity between areas of higher erosion potential and low channel formation. Even if bare ground is dominating the up-slope portions of the plot, the remaining vegetation at the down-slope end of the plot can be effective at creating pools and allowing sediment to settle out of the runoff before water leaves the plot. In addition, the up-slope end of the plot should experience lower runoff volumes than the down-slope portions of plots.

Variability of Runoff and Sediment Yield Parameters

Spatial variability in infiltration rates and erosion have been reported by Ellison (1945), Gard and Van Doren (1949), and Nyhan et al. (1984). The spatial variability in soil characteristics, flow paths, depth to parent material and infiltration rates over this seemingly uniform range site probably masked any real treatment effects on the small plots. During rainfall simulation events, qualitative observations revealed significant ponding where the borders of the plots intersected sagebrush dunes. Plot borders may create artificial ponds and interrupt flow paths to a greater degree in small narrower plots than in large wider plots. Therefore, the edge effect may be lower in large plots than in small plots. In addition, larger plots should integrate more spatial heterogeneity of soil and plant characteristics, which influence runoff and sediment variability.

Summary and Conclusions

Rainfall simulations were conducted within 1 month after vegetation reduction and soil removal treatments were applied. Results within this short period indicated that soil removal and vegetation reduction treatments did not significantly affect total runoff, equilibrium runoff ratios, or any of the sediment yield parameters analyzed. However, from these short-term results, we do not conclude that vegetation reduction and soil removal will not eventually influence runoff and sediment yield. Future research at this site may reveal long-term treatment effects that were not apparent in first year results.

Because rainfall events in this sagebrush steppe are typically of short duration, measurable parameters such as time to runoff initiation and sediment yield within 10 minutes after rainfall initiation have practical value for land managers. Time to runoff initiation was significantly affected by the 43% vegetation reduction treatment, supporting findings of previous research and strengthening the argument for grazing intensities which do not reduce vegetation cover beyond this point. However, determining a vegetation reduction threshold would, at the very least, require a finer gradation of vegetation reduction treatments.

Almost half of the variability in sediment yield is unexplained by the independent variables measured in this study, making a meaningful prediction model difficult to obtain. Despite some statistically significant multiple regression results, we can not conclude that factors affecting sediment yield in the first 10 minutes (ie., forb cover and sand in the upper soil profile) would be reliable field indicators of erosion potential in this ecosystem. While the negative correlation between sand in the upper soil profile and sediment yield was an intuitive result, interpreting the negative correlation between forb cover and sediment yield was not attempted. Though this correlation was statistically significant, further research is necessary to confirm that such a correlation is ecologically valid.

Soil surface and vegetation parameters are inherently variable in sagebrush steppe and other plant communities. Many of these parameters, such as connectivity of flow paths, are difficult to quantify and may greatly influence results. Without quantifying the connectivity of flow paths, researchers employing rainfall simulators will continue to be challenged to find treatment differences as influenced by vegetation cover and soil parameters. Future studies should consider quantifying flow path connectivity, increasing replications and improving blocking structure to more accurately determine the factors that control runoff and erosion processes in sagebrush steppe rangelands.

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J. Range Manage.
56: 159-166 March 2003

Woody vegetation response to various burning regimes in South Texas

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Abstract

Responses of woody plant communities on native rangelands in the western South Texas Plains to fire are not clearly understood. Our objective was to compare woody plant cover, density, and diversity on burned and nontreated rangelands. Five rangeland sites that received 2 dormant-season burns, 5 rangeland sites that received a combination of 1 dormant-season and 1 growing-season burn, and 5 sites of nontreated rangeland were selected on the Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Tex. Woody plant cover was estimated using the line intercept method, and stem density was estimated in 25-x 1.5-m plots. Species richness did not differ among treatments. Percent woody plant cover was reduced by 50 and 41% on winter and winter-summer combination burned sites, respectively. Honey mesquite (*Prosopis glandulosa* Torr.), twisted acacia (*Acacia schaffneri* S. Wats.), Texas persimmon (*Diospyros texana* Scheele), lotebush [*Ziziphus obtusifolia* (Hook.) T. & G.], wolfberry (*Lycium berlandieri* Dunal), and tasajillo (*Opuntia leptocaulis* Cand.) canopy cover was greatest on nontreated sites. Woody plant density declined by 29 and 23% on winter and winter-summer combination burned sites, respectively. Density of guayacan (*Guajacum angustifolium* Engelm.), wolfberry, and tasajillo was less on all burning treatments. Percent cover of spiny hackberry (*Celtis pallida* Torr.) and density of Texas pricklypear (*Opuntia engelmannii* Salm-Reif.-Dyck) declined on winter burned sites. Inclusion of summer fire into the burning regime did not increase declines in woody plants. Fire created a post-fire environment which resulted in the decline of many woody plant species. It is unclear to what degree other environmental factors such as herbivory and competition between woody plants and among woody and herbaceous vegetation may have interacted with fire in producing woody plant declines. Fire may be a useful tool in managing woody vegetation on native south Texas rangelands, while maintaining woody plant diversity.

Resumen

La respuesta de las comunidades arbustivo-leñosas de los terrenos de pastizal de las planicies del suroeste de Texas al fuego prescrito no ha podido ser entendida claramente. El objetivo de este estudio fué comparar la cobertura, densidad, y diversidad de plantas arbustivo-leñosas en áreas tratadas con fuego prescrito y en áreas no tratadas. Quince sitios fueron seleccionados en el Area de Manejo de Fauna Silvestre Chaparral ubicada en los condados de Dimmit y La Salle en Tex.: 5 sitios recibieron fuego prescrito en 2 ocaciones, ambas durante la estación de dormancia (invierno); otros 5 sitios recibieron fuego prescrito en 2 ocasiones, una vez durante la estación de dormancia y otra durante la estación de crecimiento activo (verano); y 5 sitios no recibieron tratamiento. La cobertura de plantas arbustivo-leñosas se estimó por medio del método de intercepción de linea, y la densidad de área basal se estimó usando parcelas de 25 x 1.5-m. El parámetro de riqueza de especies fué similar entre tratamientos. El porcentaje de cobertura de plantas arbustivo-leñosas se redujo en 50% en los sitios tratados en el invierno y en 41% y en los sitios tratados en invierno y verano. La cobertura del dosel de especies como *Prosopis glandulosa* Torr., *Acacia schaffneri* S. Wats., *Diospyros texana* Scheele, *Ziziphus obtusifolia* (Hook.) T. & G., *Lycium berlandieri* Dunal, y *Opuntia leptocaulis* Cand. fué mayor en sitios no tratados. La densidad de plantas arbustivas se redujo en 29% en los sitios tratados en el invierno y en 23% en los sitios tratados en invierno y verano. La densidad de *Guajacum angustifolium* Engelm., *Lycium berlandieri* Dunal, y *Opuntia leptocaulis* Cand. fué menor en todos los sitios que recibieron tratamiento. El porcentaje de cobertura de *Celtis pallida* Torr. y la densidad de *Opuntia engelmannii* Salm-Reif.-Dyck se redujo en los sitios tratados durante el invierno. La aplicación de fuego prescrito durante el verano no contribuyó a la reducción del núnero de especies arbustivas. El ambiente creado por el fuego después de su aplicación, resultó en la reducción de muchas especies arbustivas. El grado de interacción entre el fuego prescrito y otros factores ambientales, como los herbívoros, la competencia entre plantas arbustivas y entre plantas arbustivas y vegetación herbacea, en la reducción de plantas arbustivas, no es del todo claro. El fuego prescrito pudiera ser una herramienta muy útil en el manejo de la vegetación arbustivo-leñosa de los pastizales nativos del sur de Texas, y en el mantenimiento de su diversidad.

Key Words: fire, diversity, range improvement, wildlife habitat.

The Rio Grande Plains of South Texas is the southern most extension of the Great Plains Grasslands. Fire, along with other climatic variables such as drought presumably maintained the mesquite (*Prosopis glandulosa* Torr.) savannas and interspersed grasslands of pre-European settlement South Texas (Scifres and Hamilton 1993). Frequency of fire appeared to be highly variable and ranged from 5–30 years (Wright and Bailey 1982). Following European settlement, suppression of fire combined with heavy livestock grazing lead to the current thorn woodlands common

Manuscript accepted 14 Jun. 02.

throughout South Texas (Archer et al. 1988, Archer 1994).

Beginning in the mid-twentieth century, South Texas landowners began to convert thorn woodlands back to grasslands to enhance rangelands for livestock production. Mechanical treatments such as root plowing were commonly used to achieve this goal. However, once treated rangelands are revegetated by woody species, woody plant diversity can be greatly reduced (Fulbright and Beasom 1987, Ruthven et al. 1993). In South Texas, woody plants are a primary component of white-tailed deer (*Odocoileus virginianus* Boddaert) diet (Arnold and Drawe 1979, Taylor et al. 1997). Woody plants are also an important cover source for northern bobwhite (*Colinus virginianus* L.) (Guthrey 1986), and woody plants provide escape cover and thermal refugia to species of concern such as the Texas tortoise (*Gopherus berlandieri* Stejneger) (Kazamier 2000) and Texas horned lizard (*Phrynosoma cornutum* Gray) (Burrow et al. 2001).

Land ownership and land use practices in South Texas have changed in recent years. The size of individual landholdings has decreased and revenue derived from ranch properties has become increasingly dependent on wildlife rather than traditional livestock operations (Wilkins et al. 2000). Fall and winter burning along the transition zone between the South Texas Plains and Gulf Prairies and Marshes can reduce brush cover while maintaining woody plant diversity (Box and White 1969) and increase herbaceous vegetation preferred by wildlife (Box and White 1969, Hansmire et al. 1988). Fire can also provide an economical means of controlling woody species and maintaining the life of mechanical and chemical brush management treatments (Scifres and Hamilton 1993). Burning during late winter and early spring is recommended for achieving many goals on South Texas rangelands (Scifres and Hamilton 1993). As a result of reported benefits, South Texas rangeland managers are beginning to utilize fire to enhance wildlife habitat; yet, little information is available on the response of vegetation to fire in the more xeric areas of the western Rio Grande Plains. Concerns have arisen that dormant-season fire may adversely affect species of concern such as the Texas horned lizard, which hibernate at shallow depths in South Texas (Fair and Henke 1997) and that burning during summer when species such as the Texas horned lizard are active may reduce direct mortality. Summer wildfire can severely damage woody plants (Cable 1965), suggesting that controlled growing-season fire may provide an effective means of managing woody vegetation. Data on the effects of summer fire on vegetation and wildlife in South Texas are lacking.

Our objective was to determine the effects of combinations of dormant and growing-season fire on woody plant diversity, canopy cover, and density on native rangelands in the western South Texas Plains. We hypothesize that prescribe burning these South Texas rangelands will reduce woody cover while maintaining woody plant densities and diversity and that incorporation of summer fire will result in increased reductions of woody plants.

Materials and Methods

The study area was on the Chaparral Wildlife Management Area (28° 20' N, 99° 25' W) in the western South Texas Plains. The study area was purchased by the state of Texas in 1969, and is managed by the Wildlife Division of the Texas Parks and Wildlife Department (TPWD). Climate is characterized by hot summers and mild winters with an average daily minimum winter (January) temperature of 5° C, an average daily maximum summer (July) temperature of 37° C, and a growing season of 249 to 365 days depending on freezing temperatures (Stevens and Arriaga 1985). Precipitation pattern is bimodal with peaks occurring in late spring (May–June) and early fall (September-October). The 11-year (1989-2000) average precipitation amount is 54 cm (TPWD, unpubl. data).

Treatments consisted of 2 winter prescribed burns (winter burn), a winter burn followed by a summer fire (winter-summer burn), and nontreated rangeland sites. Each treatment was replicated 5 times and arranged in a randomized block design. All study plots were about 2-ha in size. Study plots were interspersed among 4 pastures in the central portion of the study area and each plot separated by > 500-m. Pretreatment sampling was not conducted; however, total woody plant canopy cover and composition of dominant woody species was considered similar among study plots prior to application of burning treatments (Gabor 1997). Burned plots were located within larger (> 50-ha) areas that were burned. Study plots and surrounding rangeland subjected to fire were burned simultaneously during each burning application. All study plots received 100% coverage by burns. All burned plots were subjected to fire during winter (December–March) 1997–1998. Winter burn plots were again burned in winter (November–January) 1999–2000. A summer fire was applied to winter-summer burn plots in August 1999. Relative humidity and air temperature, using a sling psychrometer, and surface wind speed, using the Bufort Scale, were estimated before ignition and at the completion of each fire. Relative humidity was 21 ± 3% ($\bar{x}$ ± SE), 20 ± 1%, and 32 ± 0%, temperature was 23 ± 2° C, 22 ± 3° C, and 39 ± 0° C, and wind speed was 13 ± 2 kph, 10 ± 2 kph, and 8 ± 0 kph for 1997-1998 winter burns, 1999–2000 winter burn applications, and 1999 summer burns, respectively. Relative humidity and air temperature during winter fires followed recommended prescriptions for the vegetation type present (Wright and Bailey 1982), while wind speed was slightly below recommended parameters. Little prescription data is available for summer burning in South Texas; however, 35° C is generally considered the upper limit for most prescribed burning (Wright and Bailey 1982). In South Texas, adequate humidity levels for burning are generally not reached until air temperatures are in excess of the recommended maximum. Wind direction was variable. Soil moisture was not recorded. No significant (> 0.4-cm) precipitation events were recorded within a 30-day period prior to winter burns and we considered soil moisture low. Summer burns were conducted 3 to 5 days following a 23-cm rainfall event and soil moisture was considered high. Summer burns were conducted under moist soil conditions because summer burning with little soil moisture can result in significant mortality of perennial grasses (Scifres and Duncan 1982). Because of variable wind speed and direction during all burns and uneven fuel loads, fire behavior was highly variable and not recorded. Fuel loads appeared to vary within study plots. Previous work on the study site in which fuel loads were estimated by clipping above ground biomass indicate that adequate fuel loads for burning in western portions of South Texas are ≥ 2,000 kg/ha (TPWD, unpubl. data). Based on our visual estimations, fuel loads on study plots met adequate levels. All burns were ignited as head fires with drip torches.

Soils were similar among treatments and consisted of Duval fine sandy loam, gently undulating, Duval loamy fine sand, 0–5% slopes, and Dilley fine sandy loam, gently undulating (Stevens and Arriaga 1985, Gabriel et al. 1994). The Duval series are fine-loamy, mixed, hyperthermic Aridic Haplustalfs and the Dilley series are loamy, mixed, hyperthermic shallow Ustalfic Haplargids. Topography is nearly level to gently sloping and elevation ranges between 168 and 180-m.

Vegetation is characterized by a two-phase pattern of shrub clusters scattered throughout a grassland/savanna (Whittaker et al. 1979, Archer et al. 1988). Plant communities belonged to the Honey mesquite-Spiny hackberry (*Celtis pallida* Torr.) association (McLendon 1991). Within this association were 2 primary communities, the Honey mesquite-Lime pricklyash [*Zanthoxylum fagara* (L.) Sarg.]/Spiny hackberry community, in which lime pricklyash and brasil (*Condalia hookeri* M. C. Johnst.) are the subdominants, and the Honey mesquite-Spiny hackberry/Hog-plum (*Colubrina texana* T. & G.) community, in which hog-plum is the subdominant. Prominent herbaceous species included Lehmann lovegrass (*Eragrostis lehmanniana* Nees), an introduced perennial, hooded windmillgrass (*Chloris cucullata* Bisch.), hairy grama (*Bouteloua hirsuta* Lag.), partridge pea [*Chamaecrista fasciculata* (Michx.) Greene], and croton (*Croton* spp. L.).

No record exists of the study plots being burned before the application of fire during winter 1997–1998. Domestic livestock have grazed the study area since the 18th century (Lehmann 1969). Cattle have been the major species of livestock since about 1870, whereas sheep were grazed from about 1750 to 1870. Grazing strategies on the study area have varied from continuous grazing to various rotational grazing systems (Ruthven et al. 2000). Since 1990, including the timeframe of this study, the study area has been grazed using stocker cattle under a high intensity, low frequency grazing system during the period October through April. Stocking rate was 25 animal-unit days ha^{-1} $year^{-1}$.

Three, north to south oriented, 100-m transects, were uniformly distributed on each study plot. Ten, 25-m lines were placed at 10-m intervals along each transect. Lines were oriented perpendicular to transects and direction of each line was randomly chosen by coin flip. Woody plant canopy cover was estimated during late spring and early summer 2001 by the line-intercept method (Canfield 1941). Woody plant density was estimated by counting stems in 25-x 1.5-m plots placed along each 25-m line. Frequency of occurrence of individual species was also estimated in 25-x 1.5-m plots and used to estimate species richness, diversity, and evenness. Woody species diversity (H') and evenness (J') was quantified with Shannon's Index (Pielou 1975). Because of their woody growth form in South Texas, succulents such as pricklypear (*Opuntia* spp. Miller) and suffrutescents including lantana (*Lantana* spp. L.) were considered woody plants in this study. Scientific names of Texas plants follow Jones et al. (1997) and common names are from Hatch et al. (1990).

Percent canopy cover, density, and frequency of occurrence of woody species were evaluated at the transect level using multivariate analysis of variance (MANOVA), with treatment as the main effect. Two-treatment comparisons were not conducted due to limited sample size. Tukey's HSD was used to compare individual treatments where univariate tests indicated significant ($P < 0.05$) treatment effects on individual species. Total woody plant canopy cover and total stem density, as well as species richness and Shannon's index of species diversity and evenness were calculated at the treatment level and analyzed by a 1-way analysis of variance (ANOVA) with treatment as the main effect. Tukey's HSD was used to compare treatment means. Treatment differences were considered significant at the $P < 0.05$ level.

Results

Shannon's index of species diversity varied ($P = 0.0267$) among treatments.

Table 1. Mean woody plant canopy cover (%) on winter burned[1], winter-summer burned[2], and nonburned sites[3] on the Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Tex. 2001.

Species	Winter burn	Winter-summer burn	Nonburned
		(%)	
Guajillo	0.2a[4]	0a	0a
Catclaw Acacia	1.0a	0.1a	0.3a
Huisache	<0.1a	<0.1a	0.1a
Blackbrush	0.4a	0a	0a
Twisted Acacia	1.3a	0.7a	2.7b
Whitebrush	0.1a	<0.1a	0.6a
Goatbush	0a	0a	<0.1a
Sugar Hackberry	0a	0a	<0.1a
Spiny Hackberry	0.6a	1.9b	2.2
Hog-plum	6.1a	7.1a	9.5
Brasil	3.1a	3.6a	3.9a
Texas Persimmon	0.7a	1.4ab	2.5b
Vine Ephedra	0a	0a	0a
Narrowleaf Forestiera	0.2ab	0a	0.6b
Guayacan	0.1a	0.1ab	0.5b
Tatalencho	0a	<0.1a	<0.1a
Leatherstem	0a	<0.1a	0.2a
Coyotillo	0.8a	0.2a	1.0a
Veinyleaf Lantana	0.1a	0a	0a
Common Lantana	1.6a	3.5a	2.5a
Wolfberry	0.2a	0.1a	0.9b
Texas Pricklypear	1.1a	1.7a	2.0a
Tasajillo	0.1a	0.2a	1.2b
Honey Mesquite	3.8a	5.5a	11.5b
Little-leaf Sumac	0.1a	0a	0a
Desert Yaupon	0.1a	0.1a	0.4b
Coma	<0.1a	<0.1a	0.3b
Lime Pricklyash	0.6a	<0.1b	0.1b
Lotebush	<0.1a	0.1a	0.7
Total canopy coverage[5]	22a	26a	44b

[1]Sites burned during winter 1997-1998 and winter 1999–2000.
[2]Sites burned during winter 1997-1998 and summer 1999.
[3]n = 15 transects/site/treatment.
[4]Cover values for a species across treatments followed by the same letter are not significantly different ($P > 0.05$).
[5]n = 5 sites/treatment.

Table 2. Mean woody plant density (stems/ha) on winter burned[1], winter-summer burned[2], and nonburned sites[3] on the Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Tex. 2001.

Species	Winter burn	Winter-summer burn	Nonburned
	(stems/ha)		
Guajillo	2a[4]	0a	0a
Catclaw Acacia	121a	25a	36a
Huisache	2a	0a	5a
Blackbrush	16a	0a	0a
Twisted Acacia	178a	94a	204a
Whitebrush	14a	0b	94a
Goatbush	0a	0a	11a
Sugar Hackberry	0a	0a	2a
Spiny Hackberry	116a	140ab	208b
Hog-plum	731a	665a	526a
Brasil	128a	87a	128a
Texas Persimmon	67a	113a	194a
Vine Ephedra	0a	5a	2a
Narrowleaf Forestiera	16ab	0a	27b
Guayacan	7a	7a	85b
Tatalencho	0a	0a	0a
Leatherstem	5a	23a	119a
Coyotillo	52a	14a	50a
Veinyleaf Lantana	4a	0a	0a
Common Lantana	485a	745a	644a
Wolfberry	27a	9a	82b
Texas Pricklypear	683a	1,001ab	1,095b
Tasajillo	23a	30a	187b
Honey Mesquite	242a	238a	304a
Little-leaf Sumac	4a	0a	2a
Desert Yaupon	5a	12a	44b
Coma	44a	7a	21a
Lime Pricklyash	34a	2a	21a
Lotebush	12a	20a	53b
Total woody plant density[5]	3,018a	3,237a	4,144b

[1]Sites burned during winter 1997-1998 and winter 1999–2000.
[2]Sites burned during winter 1997-1998 and summer 1999.
[3]n = 15 transects/site/treatment.
[4]Cover values for a species across treatments followed by the same letter are not significantly different ($P > 0.05$).
[5]n = 5 sites/treatment.

Diversity did not differ between winter (2.33 ± 0.13) ($\bar{x}$ ± SE) and winter-summer (2.13 ± 0.09) burning treatments whereas diversity on nonburned sites (2.55 ± 0.04) was greater than winter-summer burned treatments. Species richness and evenness did not differ among winter burned (16 ± 2 species/treatment, 0.85 ± 0.02, respectively), winter-summer burned (13 ± 2, 0.85 ± 0.01), and nonburned (18 ± 1, 0.88 ± 0) treatments. Percent woody plant canopy cover differed between treatments (MANOVA $P \leq 0.0001$). Percent total woody plant canopy cover was greatest ($P = 0.0002$) on nonburned plots (Table 1). Total woody plant cover did not differ among winter and winter-summer burned plots. Honey mesquite, wolfberry (*Lycium berlandieri* Dunal), twisted acacia (*Acacia schaffneri* S. Wats.), Texas persimmon (*Diospyros texana* Scheele), lotebush [*Ziziphus obtusifolia* (Hook.) T. & G.], desert yaupon (*Schaefferia cuneifolia* Gray), coma [*Sideroxylon celastrinum* (Kunth) Penn.], and tasajillo (*Opuntia leptocaulis* Cand.) canopy cover was greatest on nonburned plots. Spiny hackberry cover was greatest on nonburned and winter-summer burn plots. Guayacan (*Guajacum angustifolium* Engelm.) cover was greatest on nonburned plots, which did not differ from winter-summer burned plots. Canopy cover of narrowleaf forestiera (*Forestiera angustifolia* Torr.) was greatest on nonburned plots, which did not differ from winter burned plots. Lime pricklyash canopy cover was highest on winter burned plots. Density of woody species differed between treatments (MANOVA $P = 0.0004$). Total woody plant densities varied ($P = 0.0077$) by treatment with nonburned having greater densities than burned plots (Table 2). Density of wolfberry, lotebush, desert yaupon, guayacan, and tasajillo was highest on nonburned plots. Spiny hackberry and Texas pricklypear (*Opuntia engelmannii* Salm-Reif.-Dyck) density was highest on nonburned plots, which did not differ from winter-summer burned plots. Density of narrowleaf forestiera was greatest on nonburned plots, which did not differ from winter burned plots. Density of whitebrush [*Aloysia gratissima* (Gill. & Hook.) Tron.] was greatest on winter burned and nonburned plots. Frequency of occurrence values varied between treatments (MANOVA $P = 0.0080$) and followed similar trends as density estimates with the exception of lime pricklyash, Texas pricklypear, whitebrush, and spiny hackberry (Table 3). Lime pricklyash was most commonly encountered on winter burned plots; Texas pricklypear had greatest frequency of occurrence on winter-summer burned and nonburned plots; whitebrush was most common on nonburned plots, which did not differ from winter burned plots; and spiny hackberry did not differ among treatments.

Discussion

Our results indicate that combinations of dormant and growing-season burning of South Texas rangelands can effectively reduce woody plant cover and decrease certain woody plant densities. It should be noted that rangeland fire in southern Texas typically produces a mosaic of burned and nonburned areas as a result of uneven fuel loads (Box and White 1969), and the 100% coverage by fire on our study sites may not be typical of large-scale application of prescribed fire in much of South Texas. As edaphic characteristics can influence fire effects (Hansmire et al. 1988), care should be exercised when extrapolating these results to other soil types in South Texas. Prescribed burning studies conducted on clay soils in southern Texas (Box et al. 1967, Box and White 1969) are the most in-depth studies upon which regional comparisons can be made. Our observed declines in many woody species following fire were similar to those reported by Box et al. (1967) and Box and White (1969); however, Box et al. (1967) also reported decreases in brasil following September burns, which did not concur with the results of this study. The lack of a reduction of some woody species may be a result of less fuel load and variation in soil type or differences in grazing practices. Fuel loads on rangelands along the transition zone between the South Texas Plains and Gulf Prairies and Marshes can exceed 5, 476 kg/ha (Hansmire et al. 1988), which can produce more intense fires (Stinson and Wright 1969, Britton and Wright 1971) and possibly higher top-kill and mortality of woody species.

Table 3. Frequency (%) on winter burned[1], winter-summer burned[2], and nonburned sites[3] on the Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Tex. 2001.

Species	Winter burn	Winter-summer burn	Nonburned
	(%)		
Guajillo	1a[4]	0a	0a
Catclaw Acacia	12a	4a	3a
Huisache	1a	0a	2a
Blackbrush	4a	0a	0a
Twisted Acacia	36a	24a	39a
Whitebrush	4ab	0a	11b
Goatbush	0a	0a	1a
Sugar Hackberry	0a	0a	1a
Spiny Hackberry	24a	29a	33a
Hog-plum	67a	57a	58a
Brasil	29a	19a	27a
Texas Persimmon	17a	27a	26a
Vine Ephedra	0a	1a	1a
Narrowleaf Forestiera	3ab	0a	9b
Guayacan	1a	1a	16b
Tatalencho	1a	0a	1a
Leatherstem	1a	2a	7a
Coyotillo	9a	3a	13a
Veinyleaf Lantana	1a	0a	0a
Common Lantana	55a	62a	59a
Wolfberry	5a	3a	19b
Texas Pricklypear	76a	91b	91b
Tasajillo	7a	7a	44b
Honey Mesquite	51a	51a	57a
Little-leaf Sumac	1a	0a	1a
Desert Yaupon	2a	3a	12b
Coma	7a	2a	5a
Lime Pricklyash	11a	1b	2b
Lotebush	5a	6a	13b

[1]Sites burned during winter 1997-1998 and winter 1999-2000.
[2]Sites burned during winter 1997-1998 and summer 1999.
[3]n = 15 transects/site/treatment.
[4]Frequency values for a species across treatments followed by the same letter are not significantly different (P > 0.05).

Reductions of diversity on winter-summer burned plots compared to nonburned plots may not accurately reflect actual responses to fire. Shannon's index of species diversity was considerably lower on 1 winter-summer burned plot compared to the other 4 replications. This may reflect pretreatment differences among plots prior to burning. Previous vegetation mapping (Gabor 1997) suggested that all study plots were similar in regards to dominant woody species and total woody plant canopy cover before application of burning treatments; however, pretreatment differences in species composition, especially less common (frequency of occurrence < 15%) species may have existed. With the exception of lime pricklyash, declines in woody plants were limited to burned plots suggesting that declines were a result of the burning treatments. Sample sizes may also have been inadequate to fully assess treatment effects on uncommon species such as lime pricklyash.

Management of mesquite (*Prosopis* spp. L.) is a primary concern of range managers throughout the southwestern United States and northern Mexico. Mesquite can be significantly reduced following fire (Box and White 1969, Wright et al. 1976, Cable 1965). Mesquite cover declined on both burning treatments but fire did not appear to induce significant mortality. As with other woody species, moderate and uneven fuel loads coupled with varying fire behavior may have produced less intense fires resulting in low mortality. Our results were similar to Heirman and Wright (1973) in which living mesquites were not killed following prescribed burns in west Texas with fuel loads similar to our study. Wood boring insect infestations may increase in trees damaged by fire facilitating burndown and mortality as a result of secondary burns (Ueckert and Wright 1974). It is unclear to what degree wood boring insects may have infested honey mesquite following initial burns; however, little honey mesquite burndown was observed during secondary fire applications. Crown sprouting by mesquite following fire is greatest in trees that exceed 5-cm in stem diameter (Cable 1965). Although not quantified, stem diameter of most honey mesquite on our study sites appear to exceed 5-cm resulting in the maintenance of some form of apical dominance. The lack of top-kill may have reduced basal sprouting leading to the observed maintenance of canopy cover reductions 2 years following the last burn application.

Cacti (*Opuntia* spp. Miller) can also be a concern of livestock and wildlife managers. While cacti are an important food source for species such as white-tailed deer (Arnold and Drawe 1979) and javelina (*Tayassu tajacu* L.) (Sowls 1997), large colonies of Texas pricklypear can result in extensive areas virtually devoid of herbaceous vegetation. The high susceptibility of tasajillo to fire was similar to other studies (Box et al. 1967, Box and White 1969, Bunting et al. 1980). Brownspine pricklypear (*Opuntia phaeacantha* Engelm.) suffers little direct mortality following burning (Heirman and Wright 1973, Bunting et al. 1980); however, tissue destruction caused by burning increases vulnerability to damage from insects, rodents, and lagomorphs which can result in high mortality 2-3 years following burns. Moderate fuel loads combined with the robust growth form of Texas pricklypear in South Texas may explain it's general resilience to fire and subsequent insect damage. Reductions of Texas pricklypear densities on winter burned plots may in part be a result of herbivory by cattle. Texas pricklypear can be an important portion of cattle diet during winter (Everitt et al. 1981). Cattle were allowed access to pastures in which burned plots were located immediately following winter burns. Cattle readily browsed freshly burned Texas pricklypear and observations were made in which the entire above ground biomass of some plants was consumed.

Winter burns were effective in reducing canopy cover of spiny hackberry, which was similar to responses observed in the transition zone between the South Texas Plains and Gulf Prairies and Marshes (Box et al. 1967). Spiny hackberry appears to survive most fire damage but recovery rates of top-growth are slower than many other woody species. Slow recovery rates may be compounded through herbivory by white-tailed deer and other herbivores. Top-removal of woody species can increase nutrient content of regrowth (Everitt 1983), which may increase utilization by herbivores (Rasmussen et al. 1983). Spiny hackberry and other woody plants such as guayacan, which declined following burns, are considered highly preferred browse of white-tailed deer (Taylor et al. 1997). Deer density on the study area during the duration of the study

Appendix Table 1. Scientific and common names of woody species.

Scientific name[1]	Common Name[2]
Acacia berlandieri Benth.	Guajillo
Acacia greggii Gray	Catclaw Acacia
Acacia minuata M. Jones	Huisache
Acacia rigidula Benth.	Blackbrush
Acacia schaffneri S. Wats.	Twisted Acacia
Aloysia gratissima (Gill. & Hook.) Tron.	Whitebrush
Castela erecta (Turpin) T. & G.	Goatbush
Celtis laevigata Willd.	Sugar Hackberry
Celtis pallida Torr.	Spiny Hackberry
Colubrina texensis (T. & G.) Gray	Hog-plum
Condalia hookeri M. C. Johnst.	Brasil
Diospyros texana Scheele	Texas Persimmon
Ephedra antisyphilitica (Berl.) Meyer	Vine Ephedra
Forestiera angustifolia Torr.	Narrowleaf Forestiera
Guajacum angustifolium Engelm.	Guayacan
Gymnosperma glutinosum (Spreng.) Less.	Tatalencho
Jatropha diocia Cerv.	Leatherstem
Karwinskia humboltiana (Schult.) Zucc.	Coyotillo
Lantana achyranthifolia Desf.	Veinyleaf Lantana
Lantana urticoides Hayek	Common Lantana
Lycium berlandieri Dunal	Wolfberry
Opuntia engelmannii Salm-Reif.-Dyck	Texas Pricklypear
Opuntia leptocaulis Cand.	Tasajillo
Prosopis glandulosa Torr.	Honey Mesquite
Rhus microphylla (Engelm.) Gray	Little-leaf Sumac
Schaefferia cuneifolia Gray	Desert Yaupon
Sideroxylon celastrinum (Kunth) Penn.	Coma
Zanthoxylum fagara (L.) Sarg.	Lime Pricklyash
Ziziphus obtusifolia (Hook.) T. & G.	Lotebush

[1]Jones et al. (1997)
[2]Hatch et al. (1990)

averaged one adult deer 18 ha^{-1} year^{-1}, which we consider below carrying capacity for these rangeland sites. It is unclear to what degree herbivores such as white-tailed deer, lagomorphs, rodents, and arthropods may have impacted regrowth of woody plants following fires.

Woody plants comprise a very small portion of cattle diet in South Texas (Everitt et al. 1981) and direct impacts of cattle grazing appear to have little impact on woody plants following fire. High intensity, low frequency grazing results in greater consumption of less-preferred forage species (Drawe 1988), which can lead to the more uniform grazing of herbaceous plants. The high intensity, low frequency grazing system employed during the dormant-season on the study area appears to reduce selective grazing and minimize any effects selective grazing pressure may have on competition between woody and herbaceous plants following fire. Deferment of grazing on the study area during the majority of the growing-season may however, increase competition between herbaceous and woody plants.

Competition among woody plants may also explain reductions in spiny hackberry and other woody plants. Declining species such as spiny hackberry, lotebush, Texas pricklypear, tasajillo, wolfberry, and desert yaupon are closely associated with honey mesquite clusters (Whittaker et al. 1979, Archer 1989). Mesquite clusters result in concentrations of woody plants relative to the interspace between clusters. Brasil, which is also a common component of shrub clusters and demonstrated little decline following fires, appears to be more efficient in competing with other woody plants within clusters. Fire increases productivity of herbaceous plants, especially forbs on South Texas rangelands (Hansmire et al. 1988, Ruthven et al. 2000), and increased competition between woody and herbaceous plants may also account for reductions of woody plants on burned plots.

Summer fire applied during periods of above normal soil moisture can result in less damage and subsequent decline of woody plants compared to dormant-season fire applied under low soil moisture conditions (Adams et al. 1982). In part, reductions of spiny hackberry and Texas pricklypear on winter burn treatments may be explained by soil moisture conditions at the time of burning. All winter burns were conducted under relatively dry conditions, which may have resulted in high temperatures at and just below the soil surface causing greater internal tissue damage. Summer burns were performed during periods of high soil moisture and may have resulted in cooler burning conditions and less cambium destruction.

Three common (frequency ≥ 25%) woody plants that appeared highly adapted to fire are twisted acacia, hog-plum, and common lantana (*Lantana urticoides* Hayek). These species are generally low growing shrubs and because of litter accumulations beneath plants, especially hog-plum and common lantana, are easily top-killed following fire. Observations were made in which top growth of many hog-plum and common lantana plants were entirely consumed by fires. Twisted acacia and hog-plum are most abundant in the interspace between honey mesquite-shrub clusters, whereas lantana (*Lantana* spp. L.) is associated with honey mesquite clusters (Whittaker et al. 1979, Archer et al. 1988). Lack of competition between twisted acacia and hog-plum and other woody plants may explain their ability for rapid recovery following fire, while common lantana appears to more effectively compete with other woody plants within clusters. The response of twisted acacia to fire was comparable to that of huisache (*Acacia minuata* M. Jones) (Rasmussen et al. 1983), which tends to be replaced by twisted acacia along the decreasing east to west precipitation gradient across the South Texas Plains.

Conclusions and Management Implications

Both burning treatments were effective at reducing honey mesquite cover, which may promote the observed increases in herbaceous vegetation following fire on South Texas rangelands (Hansmire et al. 1988, Scifres and Hamilton 1993). Summer burning following significant rainfall may be effective in managing honey mesquite, while maintaining desirable woody species such as spiny hackberry. If reducing total woody plant cover is a management goal, burning during winter following periods of little or no rainfall is recommended. Further investigation into the response of woody plants to summer fire under various environmental conditions, in particular, low soil moisture is necessary to fully evaluate the effects of summer fire on woody plants. Where feasible, prescribed burning can manage woody vegetation without dramatic reduction in woody plant diversity, which is common with many traditional mechanical treatments (Fulbright and Beasom 1987, Ruthven et al. 1993).

If managing South Texas rangelands for white-tailed deer is a desired goal, it may be beneficial to limit the use of fire in areas dominated by highly preferred species which decline following fire and target areas dominated by vulnerable less desired species and desirable fire-tolerant species. Woody plant species such as twisted acacia and common lantana, which recover quickly following fire, are not generally considered important forage species for white-tailed deer (Arnold and Drawe 1979, Taylor et al. 1997), whereas hog-plum can be a preferred browse plant (Arnold and Drawe 1979, Ruthven et al. 1994). Although less desirable browse species such as honey mesquite, wolfberry, and desert yaupon decline following fire, the importance of these species to other game and nongame wildlife is not well documented. The effects of the structural changes of woody plant communities following fire on nongame wildlife warrant further investigation.

We recommend that initial burns on native South Texas rangelands be conducted on a 2-year interval until the desired structure of woody vegetation is achieved. Once desired goals are met, maintenance burning on a 3–5 year frequency may be adequate. Grazing strategies that allow for substantial deferment to produce adequate fuels to carry fire are critical to the successful application of fire on South Texas rangelands. High intensity, low frequency grazing systems, such as that employed on the study area, appear to be the most compatible for the incorporation of fire into a management program (Drawe 1988). Other considerations to be taken into account are the highly unpredictable weather patterns in South Texas. Short-term periods of drought are common and rainfall can be highly variable between locations (Norwine and Bingham 1985). Drought can severely impact production of fine fuels necessary to carry fire and may require flexibility in burning schedules.

Honey mesquite and associated woody plants dominate rangelands throughout South Texas; yet, productivity and species composition of herbaceous plant communities can vary greatly along the decreasing east to west precipitation gradient across the region. Decreases in herbaceous vegetation may increase the utilization of woody plants by herbivores. Further research into the interaction between burning and herbivory is needed to fully assess the effects of fire and its use as a management tool on South Texas rangelands.

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J. Range Manage.
56: 167-173 March 2003

Stocking rate effects on goats: A research observation

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Abstract

Knowledge on the ecological effects of goat grazing on arid rangeland is far from complete, and specifically there is little scientific information on effects of heavy goat grazing on arid ecosystems. One objective of this study was to determine botanical composition of dairy-type goat diets on heavily (1.5 ha per goat) and lightly (15 ha per goat) grazed Chihuahuan desert range by fecal microhistological analysis. A second objective was to determine whether vegetation cover, some blood metabolites and mineral levels, as well as fertility of goats were sensitive to high grazing pressure. The lightly grazed site had more ($P < 0.05$) total foliage cover (38.6 vs 30.4%) than the overstocked pasture. Total shrubs in diets of goats was greater (86.4 vs 72.4 in the late-dry period, 78.6 vs 42.1 in late-wet period; $P < 0.05$) on the heavily stocked pasture than the lightly stocked pasture. Forbs in the diets were lower ($P < 0.10$) in the late-dry (11.4 vs 21.5%), early-wet (55.4 vs 64.0%) and late-wet period (15.0 vs 45.8%) on the heavily stocked pasture than the lightly stocked pasture. Substantially lower ($P < 0.01$) serum glucose, urea nitrogen, Zn and Mg concentration at the onset of the breeding period in goats on the heavily stocked pasture, compared to goats on the lightly grazed pasture resulted in a higher ($P < 0.01$) abortion rate (22 vs 12%) and consequently a lower ($P < 0.05$) kidding rate (42 vs 55%). We concluded that overstocking with goats greatly reduced shrub and grass cover. Also, decades of continuously high grazing pressure has forced goats to alter diet selection pattern by consuming more resinous, toxic, and coarse species. This switch was associated with a lower nutritional status, a negative daily weight gain, lower body condition score in the late-wet period, and lower fertility on heavily grazed range.

Resumen

El impacto ecológico del pastoreo de las cabras en los agostaderos áridos continua siendo un tema de debate, y todavía no existe suficiente información científica sobre el impacto del pastoreo de las cabras sobre ecosistemas áridos. Mediante la técnica microhistológica se estudió la composición botánica de la dieta de cabras mestizas lecheras mantenidas en agostaderos con alta (1.5 ha por cabra) y baja (15 ha por cabra) presión de pastoreo, en un matorral parvifolio inerme. También se determinó el efecto de la carga animal sobre la cobertura vegetal, niveles de metabolitos y minerales en la sangre y la fertilidad de las cabras. El sitio con baja densidad de cabras presentó mayor ($P < 0.05$) cobertura de vegetación (38.6 vs 30.4%). El porcentaje de arbustos fue mayor (86.4 vs 72.4 al final del periodo de sequía, 78.6 vs 42.1 al final del periodo lluvioso; $P < 0.05$) en la dieta de las cabras en el terreno con sobrepastoreo, comparado con el terreno de baja densidad de cabras. El contenido de herbáceas fue menor ($P < 0.10$) en la dieta de las cabras en el terreno con sobrepastoreo en comparación con el sito con baja densidad de cabras al final del período de sequía. Niveles más bajos ($P < 0.01$) de glucosa, urea, Zn y Mg en el suero sanguíneo en las cabras en el terreno con alta presión de pastoreo, en comparación con el terreno con baja carga animal resultó en un mayor ($P < 0.01$) porcentaje de abortos (22 vs 12%), y un menor ($P < 0.05$) porcentaje de pariciones (42 vs 55%). Se concluyó que una alta presión de pastoreo ha incrementado la utilización por las cabras de plantas resinosas, tóxicas y fibrosas. Este cambio se refleja en un estatus nutricional más bajo, lo cual conduce a pérdidas de peso y condición corporal en el otoño, lo cual a su vez provoca una menor fertilidad de las cabras.

Key Words: Diets, blood chemistry, fertility, vegetation cover, Chihuahuan desert

In arid and semi-arid zones of Mexico, goats are managed under traditional extensive village systems and are grazed on natural communal range throughout the year with no supplements. Thus, the typical goat production system involves concentration of several large herds of goats in the communities and often surpasses the carrying capacity of these rangelands. The result is a severely overgrazed range in poor condition. An increase in stocking pressure generally represents a decrease in quantity and/or quality of forage available to the grazing animals. Few studies have described the relation between goat stocking and diet composition. Studies with Angora goats have shown that although average annual diets were similar on lightly and heavily grazed ranges, periodic differences in dietary botanical composition resulted from the 2 grazing treatments (Malechek and Leinweber 1972). Owens (1991) indicated that as goat density increased, utilization in the 0.75–1.5 m zone of Acacia shrubs community increased at a faster rate than in any other canopy zones. Provenza and Malechek (1984) found that goats showed preference for basal twigs of blackbrush in heavily stocked pastures, whereas no preference for terminal or basal twigs was observed in lightly and moderately stocked pastures. Knowledge of dairy-type goat diets under different stocking pressures remains incomplete, therefore the objective of the study was to describe forage selection and botanical composition of goat diets and relate disparities to stocking pressure. An additional aim of this study was to examine whether blood chemistry and fertility of goats and vegetation cover were sensitive to stocking level.

Financial support was received from World Wildlife Foundation (Project PN59).
Manuscript accepted 27 May 02.

Materials and Methods

Study Area

The study was conducted on a 2,250 and 1,050 ha site associated with 2 adjacent rural communities (2 km apart, with a fence dividing the sites) in northeast Mexico (25° 30' N, 101° 02 W). The communities had similar types of vegetation, soil, terrain and precipitation and were selected based on different grazing pressure of goats and the absence of other stock. Vegetation cover was 8 percentage points higher in the lightly stocked pasture. The rainy season extends from June to October with mean annual precipitation being 326 mm. Mean elevation of the study area is 1,700 m and average annual temperature is 18.2°C. Soils in the study site were silty and depth overlaying a limestone substrate ranged from 250 to 650 mm. The plant community was dominated by creosotebush (*Larrea tridentata* (DC.) Cov.). Other important browse species were resin-bush (*Viguiera greggii* (Gray) Blake) and lechuguilla (*Agave lechuguilla* Torr.). Major grasses were blue grama (*Bouteloua gracilis* H.B.K.) and buffalo grass (*Buchloe dactyloides* (Nutt) Engelm). Major forbs were globemallow (*Sphaeralcea angustifolia* (Cav.) D. Don.), silver-leaf nightshade (*Solanum elaeagnifolium* Cav.) and rosval (*Croton dioicus* Cav.).

Goat characteristics and management

Two flocks of goats (n = 163 and 167 for high and low stocking rate, respectively) were used in this study. Goats were of undefined genotype (milk-type) of different ages and parity with 35 to 45 kg adult live weight. All animals were reared in the same areas where they were tested, had no health intervention, and did not receive feed or mineral supplements throughout the year.

In and around settlements, land use is predominantly by goats, which are managed under a traditional extensive village system and are grazed on natural communal range throughout the year. The grazing period is approximately 8 hours daily (from 1000 to 1800 hours) and animals are tended by herdsmen. Goats are penned near the household at night without access to feed and water.

The lightly grazed area had been grazed continuously by goats at the rate of 15 ha per goat for several decades (one 150-herd goat in 2,250 ha). In the heavily grazed area the annual stocking rate averaged 1.5 ha per goat (5 different flocks totaling 700 animals in 1050 ha), and this grazing pressure has been maintained for several decades.

All does of both herds were exposed to crossbred (milk-type) bucks (3% bucks per herd) during 4 weeks in January 2000. Body condition score (5-point scale; Santucci and Maestrini 1985) were recorded at mating. Abortions and kiddings were also recorded.

In January 2000, blood samples (5 ml) from all adult goats in both flocks (n= 330) were collected from the jugular vein (vacutainer system), in the morning before grazing (14–16 hours from the last feeding). The blood samples were obtained in non-heparinized vacutainer tubes. Within 2 hours of collection the samples were centrifuged at 3,000 g for 15 minutes at room temperature. Serum was collected and stored at –20°C until analyzed for cholesterol, glucose, creatinine, urea, uric acid, total proteins, calcium, phosphorus, copper, magnesium and zinc. All blood metabolites analyses were carried out with a Coleman Junior II spectrophotometer following protocols supplied by the kit manufacturer. All minerals, except phosphorus, were determined by atomic absorption spectrophotometry. Phosphorus was determined by the method of Fiske and Subbarow (1925).

Thirty randomly selected adult lactating goats of each herd were weighed twice in the fall 1999 (22 October and 16 December). Animals were weighed after feed and water were withheld overnight.

Botanical composition of the vegetation

Vegetation sampling was carried out just before the start of feces sample collections for each of the 3 seasonal periods. Five transects, 500 m in length, were established in sites frequently grazed by goats in both the lightly and heavily grazed areas. Transects were positioned to avoid watering points and roads. Vegetation (foliage) cover data were collected along these transects in the late-dry (April), early-wet (July) and late-wet seasons (November) of 2000. The line-intercept method (Canfield 1942) was used to determine percent cover. In each transect the intercept of each plant species was summed and divided by the total length of the transect to obtain the percent cover per sampling unit (transect).

Fecal samples collection and analysis

Feces samples were collected from the rectum of 6 randomly-selected adult goats during 5 consecutive days in late-dry (spring), early-wet (summer) and late-wet (fall) periods. The same goats were used in each collection period. Samples were pooled across days within periods for each animal. The samples were oven-dried and ground through a 1-mm screen. Small subsamples were taken from the ground material and mounted in microscopic slides. Five slides from each sample were analyzed. Composition of goat diets was determined by counting the number of epidermal fragments of each species recognized in 100 microscope fields at 125x (Sparks and Malechek 1968). Some authors recommend the use of correction factors for forbs when the microhistological analysis is used, due to higher digestibility of forbs compared to grasses (Holechek et al. 1982) and their more fragile epidermal layers (Bartolome et al. 1995). However, other authors dismiss the use of correction factors on the grounds that phenological variation in digestibility is often more significant than taxonomic variation (Hansen et al. 1976). In this study correction factors for forbs were not used.

Selection values for individual plants were calculated as the ratio of each class percentage in the diet to its percentage availability (percentage cover) in the range (Taylor et al. 1980). The formula used in developing these ratings was:

$$\text{Selection value} = \frac{(\%\text{ in diet - }\%\text{ cover of total vegetation})}{(\%\text{ in diet + }\%\text{ cover of total vegetation})} \times 10$$

An index value of 0 indicated nonselective use of a forage class; values >0 or <0 indicated grazing selectivity for or against a particular species, respectively. Similarity of diets was calculated using Kulczyniski´s similarity index (Oosting 1956).

Statistical analyses

T-tests were used to compare shrub, forbs, grass and total vegetation cover between pastures within seasons (Steel and Torrie 1980). The numbers of epidermal fragments of each species were converted to percentages and transformed to arcsin (angular) prior to statistical analysis. For each individual species as well as life forms, t-tests at $P < 0.10$ were used to compare goat diets between pastures within seasons. Significant differences in selection indices were assessed using the

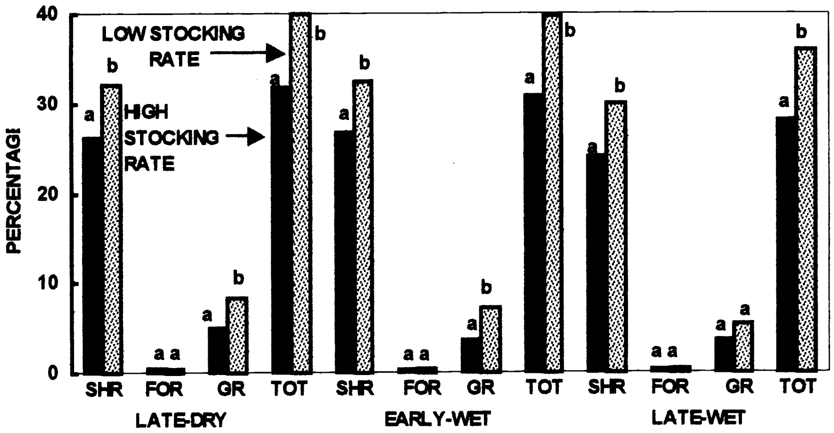

Fig. 1. Shrubs (SHR), forbs (FOR), grasses (GR) and total (TOT) vegetation cover for lightly and heavily stocked ranges in the Chihuahuan desert for 3 seasons. Paired bars with different letters differ (P < 0.05) between ranges within each sampling period.

Kruskal-Wallis test (SAS 1990). Differences in serum metabolites and minerals as well as body weight change between localities were assessed using the t-test procedure (Steel and Torrie 1980). Percentage of aborting does and proportion of does pregnant was compared using chi-square procedures (Steel and Torrie 1980). Statistical significance was assumed at $P < 0.05$). Finally, these findings depict unreplicated research (only one flock from each site) and results should be applied to other areas with some trepidation.

Results and Discussion

Vegetation cover

The lightly grazed site had significantly ($P < 0.05$) more shrub cover throughout the year than the heavily stocked pasture (Fig. 1). Because the study site was not accessible to other domestic ungulates and shrubs were generally palatable to goats, it is thought that the marked decrease of shrubs, particularly creosotebush (136% decrease cover of this shrub in the heavily grazed pasture compared to the lightly grazed pasture) on the pasture heavily grazed, arose from intensive goat grazing. This finding is consistent with that of Manzano and Navar (2000) on the reduced cover of shrubs as a result of goat overgrazing. For most of the year the grass cover was less ($P < 0.05$) on the heavily grazed compared to the lightly grazed site. Although it is known that non-Angora goats make limited use of grasses in this type of vegetation (Mellado et. al. 1991), the decrease of graminoids in the heavily grazed site was also likely due to high grazing pressure. Forb cover was very low in both sites and remained nearly the same on the two treatments. Major forbs in the study site were short-lived and dynamics were largely controlled by rainfall, rather than by grazing. In common with other studies in arid environments (Severson and Debano 1991) forbs did not increase in response to decreasing shrub cover in the heavily grazed pasture. In terms of management these results indicate that goat production would be favoured by conservative continuous grazing in this type of vegetation.

Botanical composition of diets

At the 3 seasons sampled the number of species detected in the goat diet were 34 vs 28, 30 vs 24, and 34 vs 29 on heavily and lightly grazed areas in the late-dry, early-wet and late-wet periods, respectively. The contribution of shrubs to the diet was greater ($P < 0.05$) on the heavily grazed range than the lightly grazed range in the late-dry and late-wet periods (Table 1). The predominance of shrubs (above 80%) in diets during the dry season on similar types of vegetation is consistent with Mellado et al. (1991). They found diets contained up to 93% shrubs on an overgrazed Larrea-dominated range. Higher dietary shrub content in goat diets in both the heavily and lightly stocked sites in the late-dry period was a function of decreased cover of grasses and forbs in this period. High stocking rates resulted in increased ($P < 0.05$) utilization of creosotebush by goats in the late-dry and late-wet periods. Goats on the lightly stocked site tended to avoid or consume only minor amounts of creosotebush, but goats on the heavily grazed area relied heavily on this shrub. This was a surprising finding; as it was expected that goats would not be able to cope with the chemical defenses in creosotebush. The heavy use of this resinous shrub by goats was of interest because creosotebush is generally considered unimportant and undesirable livestock forage. These results are contrary to other reports where creosote bush has been a minor diet component of Angora (Warren et al. 1984a) and Spanish goats (Mellado et al. 1991, Warren et al. 1984b). These results reaffirm that goats can live on forages rich in secondary metabolites and lignin (Provenza et al. 1990).

The relatively high consumption of poisonous plants (e.g. creosotebush, *Asclepias brachystephana* Torr. and silver-leaf nightshade) by goats on the heavily stocked range merits discussion. The tolerance for high levels of poisonous plants in goat diets probably was due to the utilization of the less-toxic portion of these plants (ruminants possess the ability to select plant parts of low toxin concentrations; Provenza 1995, Pfister 1999). However, observations on the heavily stocked pasture showed that creosotebush was uniformly and intensively used, to the point that the bark of these plants was consumed. Another explanation is that goats may have the ability to detoxify some plant poisons. Studies with desert woodrats (Mangione et al. 2000) pigmy rabbits (White et al. 1982) and goats (Duncan et al. 2000) have documented the development of mechanisms to adapt to plant secondary metabolites.

Under the heavy grazing intensity, goats consumed agrito (*Berberis trifoliolata* Moric.) and Spanish dagger (*Yucca carnerosana* (Trel.) Mckelvey), whereas in the lightly grazed area these species were not used. The high consumption of fibrous, resinous and poisonous plants by goats on the heavily stocked range reaffirm the notion that goats are very flexible with respect to the plants they consume.

Another shrub of singular importance was mesquite (*Prosopis glandulosa* Torr.), which contributed 7.8% to total composition of the diets of goats in the heavily stocked site in the late-dry period. In the late-wet period a significant grazing intensity effect ($P < 0.05$) was detected in the percentage of this shrub in the goat diets. The level of mesquite in the goat diets in the present study is much higher than that reported in other studies (Lopez-Trujillo and García-Elizondo 1995; Mellado et al. 1991). Goats on both ranges made consis-

Table 1. Percentage of shrubs, forbs and grasses in goats' diets on heavily and lightly stocked ranges.

Species	Late-dry Stocking rate		Early-wet Stocking rate		Late-wet Stocking rate	
Shrubs	High	Low	High	Low	High	Low
Acacia farnesiana	4.6	3.1	5.6	3.2	8.6	4.1
Agave lechuguilla	2.3	6.3	0.0	0.0	3.2	0.0
Agave striata	0.6+	3.3	0.0	0.7	1.0	0.0
Atriplex canescens	9.8	5.3	0.0	1.5	4.3	2.0
Berberis trifoliolata	1.6	0.0	3.0	0.0	2.7	2.5
Buddleja scordioides	1.1+	5.7	4.8	7.2	1.1**	16.3
Condalia warnockii	4.3	2.0	0.7	1.0	0.0	0.0
Cowania plicata	5.8	2.3	1.4	3.0	9.7*	0.5
Dalea bicolor	3.4	1.5	3.0	0.0	4.0*	0.2
Dasylirion palmeri	1.2*	6.3	1.2	0.7	2.6	1.7
Ephedra aspera	2.0	2.6	0.2	0.0	1.2	1.5
Larrea tridentata	15.3	7.6	6.4**	1.2	11.3**	1.5
Opuntia leptocaulis	0.4*	3.0	0.0	0.0	1.6	1.0
Opuntia rastrera	6.8	4.8	1.4	1.9	1.4	1.9
Parthenium incanum	7.9**	13.6	4.1	4.4	13.9**	1.2
Prosopis glandulosa	7.8	4.0	0.3	0.3	5.0*	2.1
Yucca carnerosana	5.9	0.0	0.0.	0.0	3.2	0.0
Other shrubs	5.6	1.0	3.0	2.5	3.8	5.6
Total shrubs	86.4*	72.4	35.1	27.6	78.6**	42.1
Forbs						
Asclepias brachystephana	4.2	0.0			0.2	0.0
Sida abutifolia	0.9	1.6	4.8	0.0	0.0	5.2
Solanum elaeagnifolium	2.6*	6.9	18.1	18.4	5.1*	17.0
Sphaeralcea angustifolia	1.5**	9.7	27.6	36	6.8**	22.1
Other forbs	2.2	3.3	4.9	9.6	3.1	1.5
Total forbs	11.4+	21.5	55.4+	64.0	15.0**	45.8
Grasses						
Aristida arizonica	1.2	0.8	0.7+	3.1	0.5*	2.4
Bouteloua curtipendula	0.2	0.7	2.4	3.8	1.8	1.9
Bouteloua gracilis	0.3	1.8	2.2	0.2	2.0	2.6
Other grasses	0.4	2.8	4.2	1.3	2.1	5.2
Total grasses	2.1+	6.1	9.5	8.4	6.4	12.1

+p = < 0.10; *p = < 0.05; **p = < 0.01 for comparisons between stocking rates within periods.

tent use of huizache (*Acacia farnesiana* (L.) Willd.) during all periods. Use of this shrub as well as mesquite by goats was somewhat limited because animals could not reach the higher canopies. Butterfly-bush (*Buddleja scordioides* H.B.K.) was significantly more important in goat diets on the lightly grazed area in the late-dry and late-wet period, compared to goats on the heavily grazed area.

Differences (P < 0.10) occurred in total forbs in goat diets on the heavily and lightly grazed areas during the late-dry and late-wet seasons (Table 1). Ralphs et al. (1986) also found that forbs declined in sheep diets as the stocking rate increased.

Major forbs in the goat diets in the heavily and lightly stocked ranges included silver-leaf nightshade and globe-mallow. These forbs were consistently higher (P < 0.05) in diets of goats on the low stocked range compared to that of heavily stocked range. Of the nearly 30 species represented in goat diets in the heavy and lightly stocked sites at the beginning of the rainy season, globe-mallow constituted one third of the diets. The abundance of forbs in the diets is explained by the fact that actively growing forbs in the Chihuahuan desert have higher protein, phosphorous, and cell soluble materials than grasses during active growth (Nelson et al. 1970).

A forb of singular importance was milkweed (*Asclepias brachystephana* Torr.), a poisonous plant which made up 4.2% of the diet during the late-dry period on the heavily stocked range, but was not present in diets on the lightly grazed site.

There were no differences in percentages of grasses in diets between stocking levels in summer and fall, but a trend (P < 0.08) was noted indicating a higher proportion of grasses in goat diets on the low stocked range in the late-dry period. Arizona three-awn (*Aristida arizonica* Vasey.) was significantly (P < 0.07) more important in diets on the lightly grazed range than the heavily stocked site in the early-wet and late-wet periods. Under the heavy grazing intensity the grass component was reduced in the late-dry period causing more dependence on shrubs.

Regardless of stocking level, utilization of grasses by goats in our study was low, which agrees with Lopez-Trujillo and Garcia-Elizondo (1995) and Mellado et al. (1991) in the same type of vegetation. Other Chihuahuan desert studies have shown much higher proportions of grasses in Spanish goat diets. Warren et al. (1984a) reported that grasses contributed over half of the diets during spring, but 17% in autumn. Warren et al. (1984b) found grass utilization by Spanish goats was between 17 and 68%.

In the Chihuahuan desert rangelands it is reported that high grazing pressure has little effect on diet selection by Angora goats (Malechek and Leinweber 1972, Taylor and Kothmann 1990). It is believed that the outstanding foraging skills of goats (upper mobile lip, bipedal grazing stance and prehensile tongue) allows selection of preferred forages even at excessive grazing pressure. Our data with milk-type goats do not support such a contention because high grazing pressure forced goats to have a more flexible foraging strategy.

Illius et al. (1999) indicated that goats select diets which tend to maximize their rate of intake, rather than expressing preferences that are specific to plant species. Moreover, hunger (Grote and Brown 1973) and social facilitation (Ralphs and Provenza 1999) rapidly extinguish food aversion. Thus, the different diet strategy showed by goats on the site with high grazing pressure apparently was an adaptation (behavioiral and physiological) to the condition imposed by grazing pressure. In other trials (Baptista and Launchbaugh 2001; Warren et al 1984b) a considerable variation between individuals with respect to voluntary consumption of unpalatable species has been found, therefore the flock on the overstocked site possibly developed an enhanced detoxification or tolerance ability. If this is true, goats with these capabilities could constitute a management strategy to increase the use of plants containing deterrents or toxicants.

Dietary preferences

The influence of stocking level on dietary selection values is shown in Table 2. In general, goats on the heavily stocked site were less selective (proportions of forage species in their diets more closely matched the proportions available), than goats on the lightly stocked range, regardless of period of the year.

Among shrubs, huizache, fourwing saltbush (*Atriplex canescens* (Pursh) Nut.),

Table 2. Selection values for shrubs, forbs and grasses of goats on heavily and lightly stocked ranges.

Species	Late-dry Stocking rate		Early-wet Stocking rate		Late-wet Stocking rate	
Shrubs	High	Low	High	Low	High	Low
Acacia farnesiana	9.7	9.5	8.5*	9.5	8.4	9.3
Agave lechuguilla	-4.6**	5.8			2.1	
Agave striata	-2.8**	4.1		2.4	9.5	
Atriplex canescens	8.9	9.1		8.2	9.5	9.3
Berberis trifoliolata	4.9		8.4		7.9	9.6
Buddleja scordioides	8.8	9.0	9.4	8.5	9.1	9.6
Condalia warnockii	7.7	8.2				
Cowania plicata	8.2*	6.5	3.2*	6.0	8.4**	3.1
Dalea bicolor	8.7	7.1	8.1		8.8	6.2
Dasylirion palmeri	8.4*	9.1	7.6	9.5	6.4	7.3
Ephedra aspera	4.3**	9.0	-5.1		6.2	7.9
Larrea tridentata	-4.6	-7.7	-8.5*	-9.6	-5.9**	-9.3
Opuntia leptocaulis	2.1*	4.3			2.7*	-2.6
Opuntia rastrera	8.6	9.4	4.0**	9.5	4.0**	9.9
Parthenium incanum	8.3	9.3	9.1	8.8	9.8**	6.1
Prosopis glandulosa	9.2*	6.4	1.9*	-3.3	7.9*	4.6
Yucca carnerosana	0.4				-0.2	
Forbs						
Asclepias brachystephana	8.7				5.5	
Sida abutifolia	7.5	8.6	8.9			8.4
Solanum elaeagnifolium	8.0	9.2	8.9	9.2	8.4*	9.6
Sphaeralcea angustifolia	8.0	9.2	7.1**	8.6	5.0**	8.7
Grasses						
Aristida arizonica	6.4+	3.7	7.7	5.6	2.3**	5.9
Bouteloua curtipendula	-1.3	2.3	3.2*	6.7	1.7	0.4
Bouteloua gracilis	-2.0	-0.6	7.3*	3.4	1.2	-1.3

+p = < 0.10; *p = < 0.05; **p = < 0.01 for comparisons between stocking rates within periods.

butterfly-bush, *Condalia warnockii* M.C. Johnst, Cowania plicata D. Don., *Dalea bicolor* H. & B. and mariola (*Parthenium incanum* H.B.K.) in both treatments and in the different seasons were eaten in proportions much higher than their relative availability would suggest. In both the heavily and lightly stocked sites creosotebush was utilized less than expected during the 3 seasons, although during the early-wet and late-wet seasons this shrub was significantly ($P < 0.05$) less preferred by goats on the lightly stocked site. Despite the avoidance shown for creosotebush, this shrub still made an important contribution to diets on the lightly grazed area.

Goats on the heavily stocked pasture showed a consistently higher ($P < 0.05$) preference for mesquite compared to goats on the lightly stocked site. Because mesquite causes conditioned flavor aversion in ruminants (Baptista and Launchbaugh 2001), it is likely that the intake of mesquite exhibited by goats on the heavily stocking pasture was not a true reflection of animal preference, but a product of forced utilization caused by a shortage of browse. The relatively high use of this shrub provoked intoxication in several goats. Signs of intoxication were mandibular tremors and uncontrolled chewing, which resulted in the death of all affected animals (7 out of 163 adult goats). These clinical signs from mesquite ingestion are caused by a selective toxicity to neurons of some cranial nerve nuclei (Tabosa et al. 2000).

Less selective grazing by goats on the heavily stock site was probably due to depletion of accessible foliage of favored species which forced the goats to turn to other less palatable choices. Walker et al. (1994) have shown that as vegetation was progressively defoliated, goats were less selective. Additionally, our goats were restricted overnight to a pen and only able to forage for 8 hours each day. This restricted foraging time probably also caused the goats to favor some of the less palatable species.

Forbs were highly preferred on both ranges, notably after summer rains. Of note, milkweed and silver-leaf nightshade, species considered toxic for livestock, were highly preferred by goats in both treatments. Forbs had higher selection values than grasses and shrubs, indicating they would have selected more forbs had they been available.

Goats in both the heavily and lightly stocked pastures showed a moderate preference for Arizona three-awn, but all others grasses were consumed in proportion to availability. The marked differences in selectivity in the lightly and heavily stocked ranges stress the fact that preferences can not be generalized because selection depends on the available choice of feed items.

Diet similarities between the heavily and lightly grazed ranges were 99, 72, and 40% for the late-dry, early-wet, and late-wet periods, respectively. The high similarity indices in the late-dry period were expected because warm-season species had not yet begun rapid growth and the least amount of forage was available. With higher forage availability (late-wet period) the similarity index was low, reflecting the effect of stocking density. Low overlap during wet times occurred when goats on the lightly stocked site concentrated more on forbs than goats on the heavily stocked site.

Blood chemistry and reproductive performance

The effect of stocking level on average daily gain, body condition score (BCS), reproductive performance and blood chemistry is presented in Table 3. A significant stocking level effect was detected for average daily gain and BCS in the late-wet season. The weight loss and lower BCS for goats on the heavily stocked site indicate a lack of nutrients in this pasture. The substantially higher ($P < 0.01$) serum glucose levels in goats on the lightly grazed area compared to the heavily grazed site is additional evidence of shortage of forage in the heavily stocked site. Glucose is a relatively good indicator of energy balance, decreasing as goats are subjected to energy restriction (Hussain et al. 1996) or fed lower levels of concentrate supplementation (Landau et al. 1993).

Serum urea nitrogen was substantially higher ($P < 0.01$) in goats on the lightly grazed area than in the heavily grazed site. This metabolite originates either from catabolism of amino acids to spare glucose oxidation, or from ammonia absorbed by the rumen (Oldham 1984). Thus, high urea levels could indicate undernutrition, reflecting increased gluconeogenesis from amino acids, or high protein intake. In this study the higher serum urea levels in goats on the lightly stocked site is believed to be due to a higher protein intake. Serum creatinine levels were lower ($P < 0.01$) in these animals, than goats on the heavily stocked site, and this metabolite is an indi-

Table 3. Daily gain, body condition score, reproductive performance and blood chemistry of goats on heavily (n = 167) and lightly (n = 163) stocked ranges. Values following ± are standard error of the mean.

Item	High stocking rate	Low stocking rate
Reproductive traits		
Abortion (%)	22 (37/167) **	12 (20/163)
Percentage kidding	42 (74/167) *	55 (90/163)
Does pregnant (%)	60 (101/167)	67 (110/163)
Mortality due to toxic plants (%)	4.2 (7/167)	0 (0/163)
Blood chemistry		
Glucose (mg/100 ml)	48.9 ± 1.3**	64.0 ± 1.1
Urea (mg/100 ml)	10.8 ± 0.33**	12.1 ± 0.29
Creatinine (mg/100 ml)	0.73 ± .05**	0.60 ± .04
Cholesterol (mg/100 ml)	66 ± 3.2+	72 ± 2.2
Total proteins (g/100 ml)	6.5 ± .13	6.8 ± .06
Calcium (mg/100 ml)	11.2 ± .16	11.0 ± .08
Phosphorus (mg/100 ml)	4.0 ± .11+	4.4 ± .09
Copper (ppm)	1.79 ± 0.06	1.83 ± 0.06
Magnesium (ppm)	1.93 ± 0.06**	2.08 ± 0.07
Zinc (ppm)	1.66 ± 0.05**	2.33 ± 0.05
Body traits		
Body condition score (0-5 scale)	2.1 ± 0.04**	2.7 ± 0.04
Average daily gain (g/d)	-19 ± 2.3**	11 ± 3.7

+p = <0.10; *p = <0.05; **p = <0.01

cator of muscle break down.

A trend ($P < 0.07$) was noted for higher serum cholesterol levels in goats on the lightly stocked site than in goats on the heavily stocked range. This metabolite, in the absence of excess dietary energy intake, is considered to reflect the capacity of the animal to mobilize body fat reserves (Ingraham and Kappel 1988). This suggests that during winter, goats on the lightly stocked site catabolized more fat reserves than goats on the heavily stocked site.

Serum phosphorus tended ($P < 0.10$) to be higher in goats on the lightly grazed area than heavily stocked site. Both serum Zn and Mg were significantly higher ($P < 0.01$) in goats on the lightly stocked site compared to goats in the heavily stocked site.

Percent of pregnant does was not significantly affected by stocking rate, but goats on the heavily stocked pasture had higher ($P < 0.01$) abortion rates and consequently lower ($P < 0.05$) kidding rates. Of the possible mechanisms inducing non-infectious abortions in the goats, the hypoglycemic condition in the mother (Wentzel 1982) was the most likely cause of gestation failure. Mean serum glucose of goats on the lightly stocked site was 31% higher than goats on the heavily stocked site. Serum Mg levels as low as ours have been associated with massive abortions in goats (Mellado et al. 2002, Unanian and Feliciano-Silva 1984).

Conclusions

The results of this study show that goat herbivory reduces shrub and grass cover in the Chihuahuan desert range when goat density is high. These results also demonstrate that decades of continuously high grazing pressure has led to divergent diet selection. Goats on the high stocking rate were forced to alter diet selection pattern by consuming more resinous (creosotebush), toxic (mesquite, milkweed) and coarse (agrito, Spanish dagger) species. This switch was associated with a lower nutritional status (lower serum glucose, urea, cholesterol, magnesium and zinc levels), weight loss, lower body condition score (BCS) in the late-wet season, and lower fertility. These results highlight the necessity of establishing conservative and flexible (seasonally) stocking densities because herbivory would reduce forage resources in areas where goat density is great, thereby setting the stage for nutritional stress and low productivity of goats.

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56: 174-184 March 2003

Mineral concentration dynamics among 7 northern Great Basin grasses

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[1]The Eastern Oregon Agricultural Research Center is jointly operated by the USDA-Agricultural Research Service and the Oregon Agr. Exp. Sta. of Oregon State University.

Abstract

Livestock and wildlife managers must be aware of the nutritional dynamics of forages to sustain satisfactory growth and reproduction of their animals and assure fair value for pasture. Despite a history of livestock grazing in the northern Great Basin, annual and seasonal mineral concentrations of many of the region's prominent grasses have not been measured. We addressed this problem with monthly sampling (April–November) of 7 cool-season grasses at 6 sites during 1992, a drier than average year (86% of mean precipitation), and 1993 when precipitation was 167% of average (255 mm). Grasses included: *Poa sandbergii* Vasey, *Bromus tectorum* L., *Sitanion hystrix* (Nutt.) Smith, *Agropyron spicatum* (Pursh) Scribn. & Smith, *Festuca idahoensis* Elmer, *Stipa thurberiana* Piper, and *Elymus cinereus* Scribn. & Merr. Phosphorus, K, Ca, Mg, Mn, Fe, Cu, Zn, and Na were assayed, and initial statistical analysis was a split-split-plot with main effects of species, years, and months and all possible interactions. For a preponderance of the minerals, (Zn and Na excluded) the 3-way year x month x species interactions were significant ($P < 0.05$) indicating that main effects did not function independently. Generally, mineral concentrations averaged about 41% higher among the grasses for the drier of the 2 years (1992). Copper, Zn, and Na concentrations were below required levels for beef cattle (9.9, 28.8, and 672 mg kg^{-1}, respectively) among all the grasses for all sampling periods. Seasonally deficient minerals included Ca, Mg, P, K, and Mn. Calcium and Mn were largely deficient (< 3.2 and 1.15 g kg^{-1}, respectively) for beef cattle early in the growing season with levels rising as grasses matured. Seasonal patterns of Mg were variable among the grasses, increasing in some as the season progressed, remaining stable among others, and declining with maturity in yet others. Phosphorus and K levels were typically adequate (>1.94 and 5.76 g kg^{-1}, respectively) for beef cattle early in the growing season and declined to deficient levels by July and August. Iron was of no concern, because concentrations were more than adequate for cattle (> 48 mg kg^{-1}) among all the grasses for all seasons. While a mixed stand of forages can extend the period of adequate mineral nutrition for cattle in some instances, we suggest that a supplement be available season-long on northern Great Basin rangelands and that the formulation include at least Ca, Mg, P, K, Cu, Zn, Mn, and Na in available forms and proper ratios.

Resumen

Los manejadores de fauna y ganado deben estar enterados de las dinámicas nutricionales de los forrajes para sostener un crecimiento y reproducción satisfactorios de sus animales y asegurar el valor favorable de sus praderas. A pesar del historial de apacentamiento de ganado en la Gran Cuenca del Norte las concentraciones anuales y estaciónales de minerales de muchos de los zacates importantes de esta región no habían sido medidas. Nosotros abordamos este problema con muestreos mensuales (Abril - Noviembre) de 7 zacates de estación fría en 6 sitios, durante 1992, un año mas seco que el promedio (86% de la precipitación promedio) y en 1993 cuando la precipitación fue 167% de la precipitación promedio (255 mm). Los zacates muestreados fueron: *Poa sandbergii Vasey, Bromus tectorum L., Sitanion hystrix* (Nutt.) Smith, *Agropyron spicatum* (Pursh) Scribn. & Smith, *Festuca idahoensis* Elmer, *Stipa thurberiana* Piper, and *Elymus cinereus* Scribn. & Merr. y los minerales determinados fueron P, K, Ca, Mg, Mn, Fe, Cu, Zn y Na. El análisis estadístico inicial fue un diseño experimental de parcelas subdivididas, en el que los efectos principales fueron las especies, años y meses y todas sus posibles interacciones. Para la mayoría de los minerales (excluyendo Zn y Na) las interacciones triples año x mes x especie fueron significativas ($p < 0.05$) indicando que los efectos principales no actúan en forma independiente. Generalmente las concentraciones de minerales promediaron aproximadamente 41% mas en los zacates del año mas seco (1992). Las concentraciones de Cu, Zn y Na estuvieron por abajo de los niveles requeridos por el ganado para carne (9.9, 28.8 y 672 mg kg^{-1}, respectivamente), esto fue para todos los zacates y todos los periodos de muestreo. Los minerales estacionalmente deficientes incluyeron al Ca, Mg, P, K y Mn. El Ca y Mn fueron muy deficientes (< 3.2 y 1.15 g kg^{-1}, respectivamente) para el ganado para carne al inicio de la estación de crecimiento y los niveles fueron incrementando conforme los zacates maduraron. Los patrones estaciónales de Mg variaron entre las especies de zacates, incrementando en algunos de ellos conforme la estación de crecimiento avanzó, permaneciendo estable en otros y disminuyendo con la madurez en otros. Al inicio de le estación de crecimiento los niveles de P y K fueron adecuados (>1.94 y 5.76 g kg^{-1}, respectivamente) para el ganado para carne y disminuyeron a niveles deficientes en Julio y Agosto. Respecto al Fe no hubo preocupación porque las con centraciones fueron más que adecuadas para le ganado (>48 mg kg^{-1}), esto fue para todas las especies y todas las estaciones. Mientras que en algunas situaciones una comunidad con

Technical Paper No. 11899 Oregon Agr. Exp. Sta.
Manuscript accepted 16 May 02.

diversas especies forrajeras puede extender el periodo de una nutrición adecuada de minerales para el ganado, nosotros sugerimos que en los pastizales de la Gran Cuenca del norte se tenga una suplementación de minerales disponible durante toda la estación y que la formulación incluya al menos Ca, Mg, P, K, Cu, Zn, Mn y Na en formas disponibles y relaciones adecuadas.

Key Words: copper, zinc, manganese, sodium, iron, phosphorus, magnesium, potassium, calcium, *Poa sandbergii, Bromus tectorum, Sitanion hystrix, Agropyron spicatum, Festuca idahoensis, Stipa thurberiana, Elymus cinereus*

Stockmen and wildlife managers must be aware of the nutritional concentrations of forages on rangelands to assure adequate growth and reproduction of their animals and make informed decisions when purchasing supplements. Similarly, those marketing pasture should also be aware of the nutritional characteristics of their forages to assure reasonable and fair returns. Despite a history of livestock grazing in the northern Great Basin, there have been few efforts to quantify the seasonal and annual mineral concentrations of the region's most prominent rangeland grasses (Murray et al. 1978, Mayland and Shewmaker 1997).

The northern Great Basin experiences an arid Mediterranean climate with about 80% of the annual precipitation occurring in the fall, winter, and spring months when low temperatures hinder plant growth. Rangeland grasses typically begin growth with warming temperatures in the spring, and herbage accumulation stops upon depletion of soil moisture in mid- to late-July (Sneva 1982, Ganskopp 1988). Hickman (1975) presented Ca and P profiles for 4 grasses common to the region, and Murray et al. (1978) and Mayland and Shewmaker (1997) described the seasonal dynamics of 9 elements for 2 introduced and 5 native grasses in southern Idaho. Neither source, however, addressed the year to year disparities in nutritive value associated with precipitation differences.

Rates of gain for livestock reflect the nutritional dynamics of the region's forages with mature cows gaining up to 1.86 kg day^{-1} early in the growing season and losing 0.4 kg day^{-1} by mid- to late-August (Raleigh and Wallace 1965, Turner and DelCurto 1991). Within the same period, calf gains may range from 0.7 to as little as 0.1 kg day^{-1} (Turner and DelCurto 1991). Mineral supplementation has not been intensively studied in this region, however, Murray et al. (1978) reported enhanced April–December gains in cattle supplemented with protein, phosphorus, and sulfur and slightly elevated gains of supplemented calves from August to December. Later, Mayland et al (1980) documented increased weight gains by grazing cattle supplemented with additional zinc.

Our objective was to characterize seasonal and annual mineral concentrations of 7 of the region's most prominent rangeland grasses. This was accomplished via monthly sampling at 6 sites during 1992, a drier than average year, and 1993 when above average precipitation occurred.

Materials and Methods

Six collection sites were identified near Burns, Ore. with each supporting a broad array of forages. Specific locations, elevations, and soil classifications for each site were reported by Ganskopp and Bohnert (2001). Among the 6 sites, mean soil depth was 69 cm (se = 5.1), and elevation ranged from 1,375 to 1,472 m ($\bar{x}$ = 1,429). Along an east/west line, the sites spanned 118 km, and north/south extremes encompassed 75 km. Climatological data reported herein were acquired at the Northern Great Basin Experimental Range (119° 42' 30"W 43° 29' 37"N) with the location identified as the Squaw Butte Experiment Station in N.O.A.A. records (N.O.A.A. 1991 through 1994).

The shrub layer at each site was dominated by Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle) with occasional occurrences (<10% relative cover) of mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* (Rydb.) Beetle) at upper elevations. Dominant perennial grasses were typically bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) or Idaho fescue (*Festuca idahoensis* Elmer). Subordinate grasses included Sandberg's bluegrass (*Poa sandbergii* Vasey), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) Smith), Thurber's needlegrass (*Stipa thurberiana* Piper), giant wildrye (*Elymus cinereus* Scribn. & Merr.), prairie Junegrass (*Koeleria cristata* Pers.), and in disturbed areas, the introduced annual cheatgrass (*Bromus tectorum* L.). All of these grasses are common in the sagebrush steppe, and with the exception of prairie Junegrass, one or another may dominate the herbaceous layer depending on site specific conditions and environmental factors (Daubenmire 1970, Hironaka et al. 1983).

We evaluated 7 grasses in this study. Among these were Sandberg's bluegrass, a small stature, early maturing, caespitose, perennial grass and cheatgrass, an early maturing winter annual. The remaining 5 perennial grasses included bottlebrush squirreltail, bluebunch wheatgrass, Idaho fescue, Thurber's needlegrass, and giant wildrye. With the exception of giant wildrye, which can attain heights of up to 2 m, these are mid-size caespitose grasses. In both years (1992 and 1993) we visited all 6 locations and sampled each within a 3-day interval at the end of each month. Months sampled included April–November in both years.

Yearly precipitation compiled on a calendar year basis at the Northern Great Basin Experimental Range was 106 and 140% of the long-term average ($\bar{x}$ = 283 mm, n = 41) for calendar years 1992 and 1993, respectively (N.O.A.A. 1992-1993). Sneva (1982), however, discovered that yearly forage yield in the region was most closely correlated with precipitation accumulated on a crop year or September through June basis. Based on that premise, accumulations for the 1992 and 1993 growing seasons at the Northern Great Basin Experimental Range were 86 and 167% of the crop year average (255 mm), respectively (Fig. 1). Both years of the study, however, experienced higher than average mid- to late-growing season rainfall. June–July precipitation totaled 68 mm in 1992 compared to an average of 34 mm. In 1993 pooled July- August precipitation

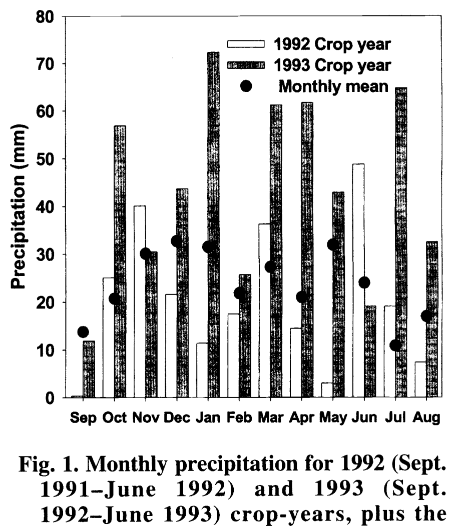

Fig. 1. Monthly precipitation for 1992 (Sept. 1991–June 1992) and 1993 (Sept. 1992–June 1993) crop-years, plus the months of July and August in 1992 and 1993, and mean monthly accumulations (n = 41) for the Northern Great Basin Experimental Range near Burns, Ore.

Table 1. P-values derived from a split-split-plot analyses of variance for mineral content of 7 grasses commonly found on northern Great Basin rangelands near Burns, Ore. Main effects were species of forage (N = 7), years (1992 and 1993), and months (Apr.–Nov.). Shaded values are not statistically significant (P > 0.05).

		Mineral								
SOURCE	DF	P	K	CA	MG	MN	FE	CU	ZN	NA
Species (S)	6	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.098	0.019
Year (Y)	1	0.003	0.045	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Y x S	6	0.001	0.182	0.018	0.002	0.173	0.186	0.006	0.003	0.270
Month (M)	7	0.001	0.001	0.001	0.001	0.004	0.001	0.001	0.001	0.001
M x S	42	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.002	0.036
Y x M	7	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
Y x M x S	42	0.009	0.001	0.001	0.001	0.010	0.002	0.046	0.261	0.388

was 97 mm exceeding the long term mean of 27.2 mm by nearly 70 mm. Mean April–July temperatures were 2.5° C warmer than average ($\bar{x}$ = 12.4° C) in 1992 and 1.6° cooler than average in 1993. A model based on precipitation accumulations for predicting annual herbage yields in the region furnished production estimates of 542 kg ha^{-1} for 1992 and 1,257 kg ha^{-1} for 1993 (Sneva 1982). For the most part the grasses exerted few reproductive stems in 1992 and exhibited a wealth of reproductive effort in 1993.

At each site, samples were harvested from at least 6 plants per species by clipping to a 2.5-cm stubble and compositing materials by species. Greater numbers of plants were used for small stature grasses like Sandberg's bluegrass. Plants at each site were sampled as they were encountered along a pace transect until adequate amounts of material were obtained. Each site experienced light (< 40% utilization) summer/fall grazing by cattle, but only ungrazed plants were included in our collections. Samples harvested before spring growth consisted of leaves and culms produced in the previous growing season. After growth initiated in the spring, crowns of the caespitose grasses were lightly crushed and the brittle and broken old-growth brushed aside before samples were collected. Plant materials were stored in labeled, paper bags in the field and transported to Eastern Oregon Agricultural Research Center headquarters where they were oven-dried at 60° C for 48 hours, ground to pass a 1-mm screen, and stored in plastic bags at room temperature for subsequent chemical assays. Samples were analyzed for calcium (Ca), phosphorus (P), magnesium (Mg), potassium (K), copper (Cu), zinc (Zn), manganese (Mn), sodium (Na), and iron (Fe). Assays were performed by The Research Extension Analytical Laboratory at The Ohio State University using Inductive Coupled Plasma (ICP) spectroscopy (Vela et al. 1993, Sirois et al. 1994). The specific instrument was an Applied Research Laboratory ICP Model 137[1]. Plant samples were dry-ashed, treated with HNO_3, dissolved in HCL, and aspirated via an argon carrier into the ICP plasma chamber where ionized elements were quantified by emission spectroscopy (AOAC 1990).

To establish a reference point for the various minerals, the required levels in forages for beef cattle were extracted from NRC (1996) requirements. The reference animal was a 5-yr old 454 kg Hereford x Angus cross cow, trailing its third 120-day old calf, 60 days post breeding, with a body condition score of 5, and consuming 2.5% (11.4 kg dry matter basis) of body weight per day.

Experimental design was a randomized complete block with 6 replications (sites) and 3 factors (years (n = 2), months (n = 8), and species of forage (n = 7)). Initial analyses employed a split-split-plot analysis of variance with species as whole-plots, years as subplots, and months as sub-subplots (Petersen 1985). The replication x species error term (30 df) tested for species effects. The replication x year x species error term (35 df) tested the main effect of years and year x species interaction. The species x year x replication x month error term (490 df) tested for main effects of months, species x month, and species x year x month interactions. Because all year main effects and 21 of 27 interactions involving year effects (Table 1) were significant P < 0.05), data were sorted by year, and each year analyzed separately employing a split-plot analysis of variance with species serving as whole plots and months as subplots. Mean separations between adjacent months within a species and year were obtained with Fisher's protected LSD procedures (Fisher 1966) with statistical significance accepted at $P \leq 0.05$. All "$\pm$" symbols within this manuscript are associated with standard errors derived from 6 observations.

[1]Tradenames are supplied for information only and do not constitute endorsement by USDA-ARS of any product to the exclusion of others that may be suitable.

Results and Discussion

Statistical analyses

With our initial split-split-plot analyses of variance, the 3-way year x month x species interaction was significant (P < 0.05) for 7 of 9 elements (exceptions were Zn and Na (Table 1)). That being the case, the 3 main effects did not function independently, and a majority of the data must be presented in a 3-way format. To briefly communicate the relative amounts of variation associated with our initial split-split-plot analyses, component variances were totaled across all 9 elements. Year, month, and species main effects respectively accounted for 42, 29, and 9% of the total variation (data not shown). Among the 2-way interactions year x species constituted 2.1% month x species 1.8%, and year x month 9.6%. The 3-way year x month x species interaction contributed 0.6%. Among error terms, number 1 (rep x species) contributed 1.0%, number 2 (species (rep x year)) contributed 0.7%, and error term 3 approximately 0.4%.

Table 2. P-values derived from separate split-plot analyses of variance for 1992 and 1993 mineral content of 7 grasses found on northern Great Basin rangelands near Burns, Ore. Main effects are species of forage (N = 7) and months (Apr.–Nov.). Shaded values are not statistically significant (P > 0.05).

		1992								
		Minerals								
SOURCE	DF	P	K	CA	MG	MN	FE	CU	ZN	NA
Species (S)	6	0.004	0.001	0.001	0.001	0.001	0.001	0.001	0.329	0.014
Month (M)	7	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
M x S	42	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.232	0.139
		1993								
		Minerals								
SOURCE	DF	P	K	CA	MG	MN	FE	CU	ZN	NA
Species (S)	6	0.001	0.001	0.001	0.001	0.001	0.002	0.001	0.001	0.012
Month (M)	7	0.001	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001
M x S	42	0.001	0.001	0.001	0.001	0.001	0.003	0.001	0.001	0.207

Replications or sites accounted for 3.7% of the total variation.

When year effects were removed from the model and each year analyzed separately, 15 of 18 month x species interactions (Table 2) were significant ($P \leq 0.01$). That being the case, species did not react similarly as we progressed from month to month within years and again data must be presented for each species at monthly intervals for the majority of the data. Two of the 3 month x species exceptions involved Na ($P > 0.13$) in both 1992 and 1993. Main effects of species and month were significant ($P \leq 0.02$), however, suggesting that while Na concentrations differed among the grasses, they responded similarly as we progressed from month to month. The third exception to a significant ($P = 0.23$) month x species interaction was Zn in 1992. Species effects were not significant ($P = 0.32$) either in that analysis suggesting that monthly means compiled across species would adequately describe Zn dynamics of the grasses in 1992. Both main effects and the month x species interaction were significant ($P < 0.01$) for Zn in 1993, however. When components of these analyses of variance were totaled across years and minerals, month effects accounted for 46% of the total variation, species of grass about 31%, replications or locations about 12.5%, the species x month interaction 4.9%, error term number 1 about 3.8%, and error term two, 1.9%. Again, given the preponderance of significant 2 and 3-way interactions in our analyses, data will be presented at monthly resolutions for each year for each species of grass.

Calcium

Among grasses and for the duration of the study, mean Ca concentration was 2.99 g kg^{-1} ($\pm$ 0.08). Given that all interactions were significant ($P < 0.05$) among all analyses, there was great variability among forages and months and between years (Fig. 2). With the exception of the winter annual, cheatgrass, most of the grasses began the growing season with a Ca content just at or below 3.2 g kg^{-1}, the concentration necessary to meet NRC (1996) requirements for beef cattle. Sandberg's bluegrass, however, never exceeded the recommended Ca level for cattle in any month of either year. Sandberg's bluegrass responded to November precipitation in 1992 with elevated ($P < 0.05$) Ca levels that approached the required level, and cheatgrass responded with significant increases ($P < 0.05$) to November rains in both years. Among the medium and large stature perennial grasses (bottlebrush squirreltail, bluebunch wheatgrass, Idaho fescue, Thurber's needlegrass and giant wildrye), however, Ca content typically peaked well above recommended levels in late-July and then declined as these grasses matured and entered quiescence. None of these 5 grasses, however, exhibited significant increases in Ca levels with the arrival of fall (October/November) moisture.

A general pattern evident among all the grasses was that Ca levels were typically higher ($P < 0.05$) during the dry 1992 growing season than the more moist 1993 months. The dilution of mineral concentrations with more favorable growing conditions is frequently seen and attributed to accumulation of more carbon under optimal conditions. Conversely, growth restriction during drought is accompanied by mineral concentration. With minimal selective grazing among these forages, cattle could have easily ingested sufficient Ca during the full 8-month sampling period of 1992. By selecting for cheatgrass early in the growing season and bluebunch wheatgrass later in the year, cattle could have potentially acquired sufficient Ca for 7 of the 8 months sampled in 1993. All of the grasses, however, were Ca deficient for cattle during the late June—July interval of 1993. Typically though, unless cattle are heavily lactating or foraging on rapidly growing herbage on acid, sandy, or organic soils, clinical signs of Ca deficiencies are rare among grazing beef cattle (Underwood 1981).

Magnesium

Pooled across years, months, and forages mean Mg content was 0.94 g kg^{-1} ($\pm$ 0.006), and the concentration necessary to meet NRC (1996) requirements was 1.15 g kg^{-1}. Like Ca, all interactions were significant ($P < 0.01$) among all 3 analyses of variance (Tables 1 and 2) again indicative that annual and seasonal Mg contents of the grasses were quite variable among year, month, and species combinations.

Cheatgrass exceeded the required level of Mg from early May to late June of both years (Fig. 3). Idaho fescue also equaled or exceeded the Mg requirements of cattle in the early growing season, and both bottlebrush squirreltail and giant wildrye fur-

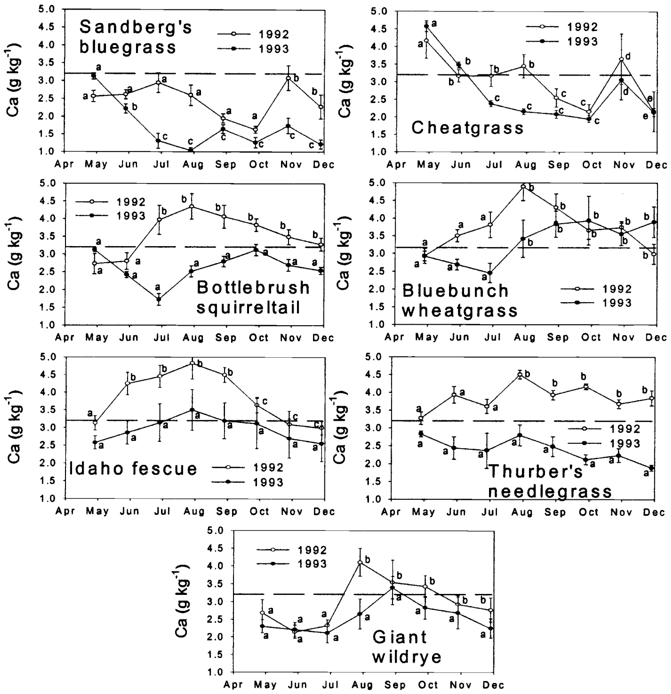

Fig. 2. Mean calcium content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes required Ca content of forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly ($P > 0.05$) different. Fisher's protected LSD ($P = 0.05$) = 0.85 and 0.84 g kg^{-1}, respectively, for 1992 and 1993.

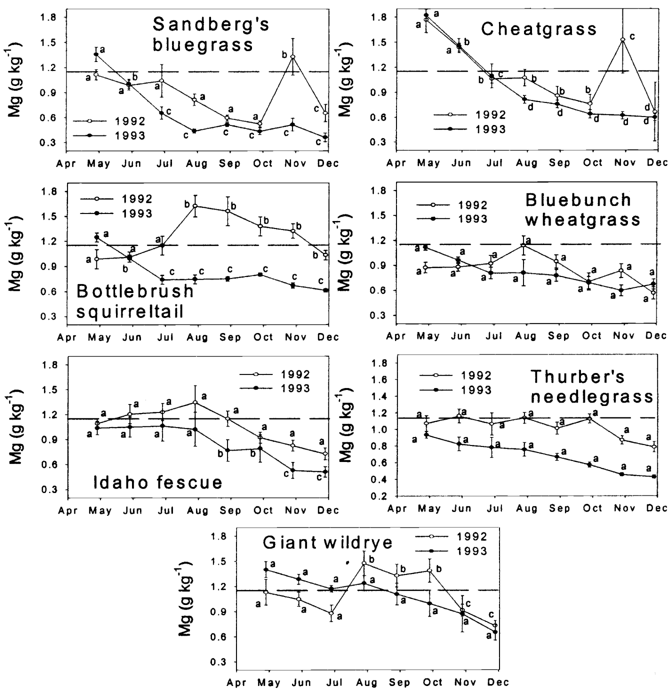

Fig. 3. Mean magnesium content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes required Mg content forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly ($P > 0.05$) different. Fisher's protected LSD ($P = 0.05$) = 0.34 and 0.24 g kg^{-1}, respectively, for 1992 and 1993.

nished adequate levels of Mg from July into November of 1992. Both Sandberg's bluegrass and cheatgrass responded to October rains with significant increases in Mg that exceeded requirements of cattle in 1992. Magnesium content of bluebunch wheatgrass marginally approached the required level for cattle for only 1-sampling period each year. Both bluebunch wheatgrass and Thurber's needlegrass were notable because neither species exhibited a significant ($P > 0.05$) month to month change in Mg content for either year. When pooled across species within years, selective grazing by cattle could have furnished adequate Mg level for all but the last 15 days of November in 1992. In 1993, however, none of the grasses provided adequate Mg from mid-August through late-November. Grass tetany generally occurs during early spring, when grasses are exhibiting rapid vegetative growth (McDowell and Valle 2000), and lactation demands of cattle are peaking. With the exception of cheatgrass, which was found primarily on disturbed sites, and giant wildrye early in the 1993 growing season, our grasses were marginally satisfactory or deficient for Mg from late-April into late June. Bottlebrush squirreltail, Idaho fescue, and giant wildrye furnished adequate Mg for the July-October period in 1992, but nearly all of the grasses were deficient beyond late-June for the 1993 growing season.

Phosphorus

Mean P concentration among grasses over the trials was 1.42 g kg^{-1} (± 0.09), and the concentration necessary to meet NRC (1996) requirements was 1.94 g kg^{-1}. Maximum and minimum values detected were 5.04 and 0.28 g kg^{-1}, respectively. While all interactions were again significant ($P < 0.01$) among all 3 analyses of variance (Tables 1 and 2), P did not exhibit the same degree of year to year variability among species and months (Fig. 4) as Ca and Mg. The general pattern among the grasses was that P levels equaled or exceeded cattle requirements early in the growing season and rapidly declined to inadequate levels by late July or early August in both years. Phosphorus levels were consistently higher ($P < 0.05$) for the early portions of the 1993 growing season than for the early months of 1992. In 1992, cheatgrass sustained adequate levels of phosphorus until mid-July, while all of the remaining grasses were largely deficient by mid-June. Sandberg's bluegrass and cheatgrass responded to October 1992 precipitation with significant ($P < 0.05$) increases in P during November, but adequate P levels for cattle were not sustained into December. The other medium stature grasses showed no significant ($P > 0.05$) responses to fall moisture in either year.

On a worldwide basis, the most prevalent mineral deficiency among livestock is probably phosphorus (Underwood 1981). Phosphorus deficiencies are more prominent among tropical grasses than temperate forages (McDowell et al. 1984), and the most devastating result of deficiency among cattle is reproductive failure (McDowell and Valle 2000). Where serious deficiencies occur, lactating cows may not enter oestrus until they cease milking or are supplemented with phosphorus (Lammond, 1970). Olson (1971) noted increased gains by cattle on southern Idaho cheatgrass ranges when phosphorus was supplemented.

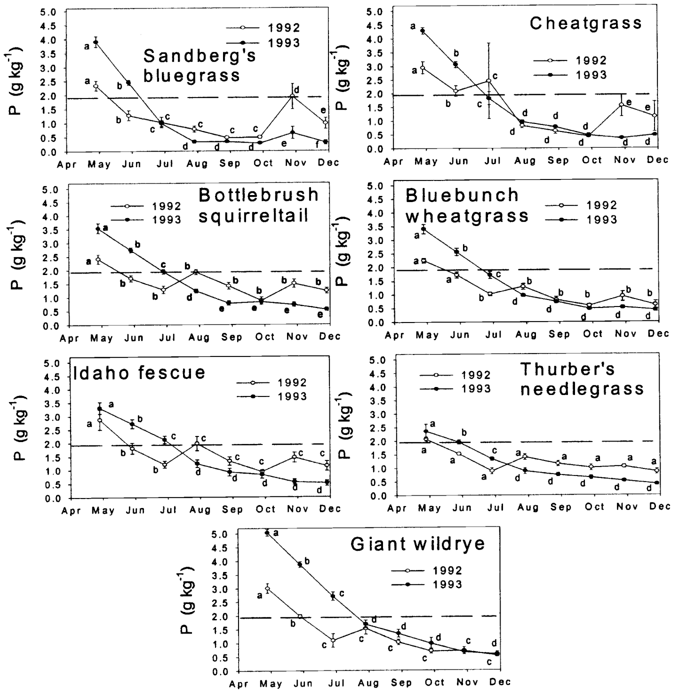

Fig. 4. Mean phosphorus content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes required P content of forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly ($P > 0.05$) different. Fisher's protected LSD ($P = 0.05$) = 0.66 and 0.34 g kg^{-1}, respectively, for 1992 and 1993.

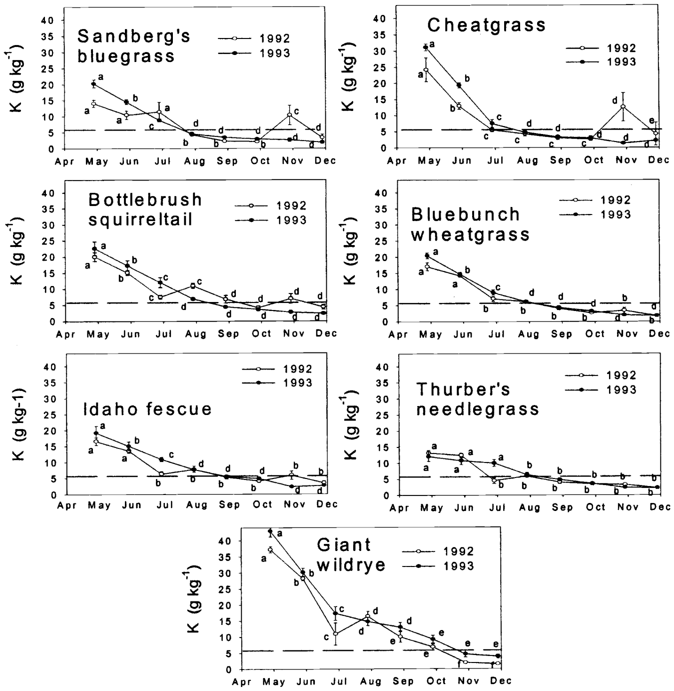

Fig. 5. Mean potassium content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes required K content of forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly ($P > 0.05$) different. Fisher's protected LSD ($P = 0.05$) = 3.77 and 2.56 g kg^{-1}, respectively, for 1992 and 1993.

Potassium

Mean K content of all forages was 9.0 g kg^{-1} (± 0.74), and seasonal values ranged from a high of 42.9 to a low of 1.39 g kg^{-1} (Fig. 5). The concentration in forages needed to meet NRC (1996) requirements for beef cattle was 5.76 g kg^{-1}. Again the significant 3-way year x month x species interaction implied that K concentrations did not respond similarly between years and that species were not similar across months. In both years, all of the grasses began the growing season with adequate K levels for beef cattle. Sandberg's bluegrass and cheatgrass were the first forages to exhibit inadequate K concentrations for cattle becoming deficient by approximately late-July in both years. Bluebunch wheatgrass, bottlebrush squirreltail, Idaho fescue, and Thurber's needlegrass, however, sustained adequate levels of K into mid-August or early September. Giant wildrye was notable because it sustained adequate amounts of K until about mid-October of both years. Both Sandberg's bluegrass and cheatgrass responded to October 1992 precipitation with increased levels ($P < 0.05$) of K. None of the other forages displayed a response to fall precipitation, and all of the grasses were K deficient by about mid- November.

McDowell and Valle (2000) found few reports of a K deficiency among ruminants foraging under natural conditions. Potassium typically exists as a cellular constituent among animals, but it occurs at much higher levels in milk than sodium. That being the case, lactating cattle can not conserve supplies as effectively as their nonlactating counterparts (Maynard and Loosli 1969). When deficiencies do occur, general symptoms include: slow growth, reduced feed and water intake, lowered feed efficiency, weakness, nervous disorders, and degeneration of vital organs. Potassium deficiencies are usually not seen, however, because associated nutrients are typically even more deficient and their symptoms manifested much sooner than those of potassium (McDowell and Valle 2000).

Copper

Copper concentration of the 7 grasses averaged 1.75 mg kg^{-1} (± 0.11). While all interactions were significant for each analysis of variance ($P \leq 0.46$), the seasonal dynamics of these grasses are of little interest, because their Cu content never approached the NRC (1996) requirement for cattle forages of 9.6 mg kg^{-1} (Fig. 6). Cheatgrass and giant wildrye consistently began the growing seasons with higher levels of Cu than the other grasses, but all of the grasses provided only 10 to 25% of the Cu required for cattle by about July or August. Idaho fescue was notable in that no significant ($P > 0.05$) month to month changes in Cu content occurred in 1992 or 1993. Seasonal dynamics were not substantial either for bottlebrush squirreltail, bluebunch wheatgrass or Thurber's needlegrass.

Availability of dietary copper to animals is affected by interactions with Mo, S, and Fe (Suttle 1981), with excesses of either retarding copper availability. A wide array of symptoms accompany copper deficiencies among cattle, and their diversity may be linked to complex interactions involving other minerals. Some of the clinical signs include: bleaching of hair, nervous symptoms (ataxia) in calves whose dams experienced deficiency during pregnancy, lameness, and swelling of joints (Maynard and Loosli 1969). Serum assays of beef cattle by Raleigh (1988) in south-east

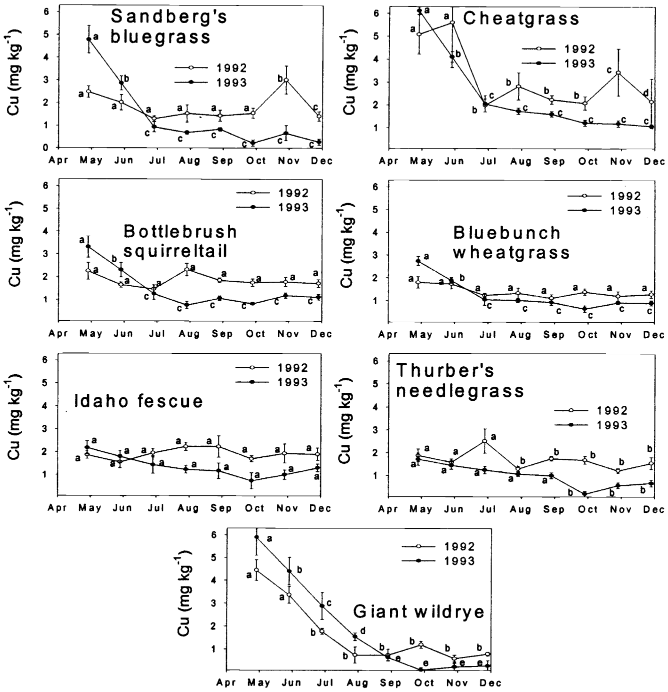

Fig. 6. Mean copper content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The required copper content of forages for a 454 kg cow is 9.6 mg kg^{-1}. Adjacent monthly means within a year sharing a common letter are not significantly (P > 0.05) different. Fisher's protected LSD (P = 0.05) = 1.19 and 0.73 mg kg^{-1}, respectively, for 1992 and 1993.

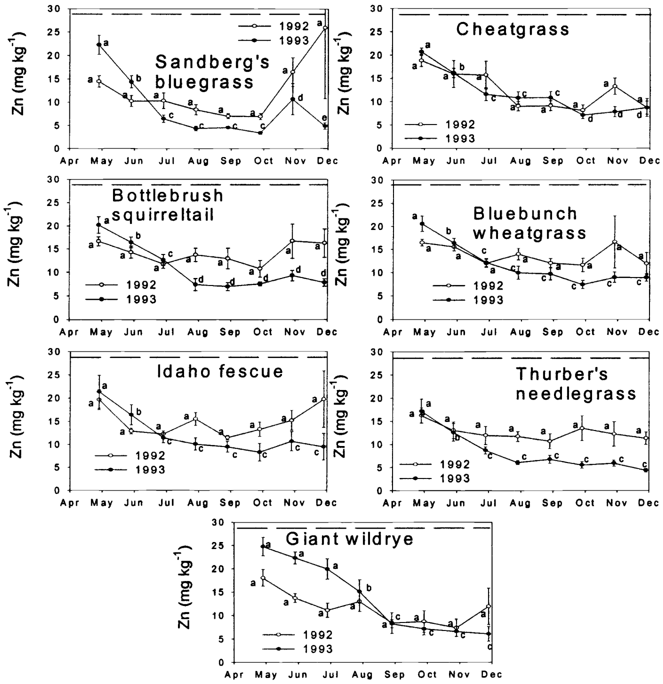

Fig. 7. Mean zinc content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The required zinc content of forages for a 454 kg cow is 28.8 mg kg^{-1} (dashed horizontal line). Adjacent monthly means within a year sharing a common letter are not significantly different (P > 0.05). Fisher's protected LSD (P = 0.05) = 7.82 and 3.75 mg kg^{-1}, respectively, for 1992 and 1993.

Oregon revealed marginal Cu levels, and up until 1988 clinical symptoms had not been noted. Recently, however, some herds in southeast Oregon have developed health and reproductive disorders attributed to Cu deficiency. Consequently, many producers have begun monitoring the Cu status of their animals and become more attentive to management of their mineral programs.

Zinc

Mean Zn content of the grasses was 12.1 mg kg^{-1} (± 0.44). With our full ANOVA model, species effects (P = 0.09) and the 3-way interaction (P = 0.26) were not significant (Table 1). When years were analyzed separately, however, all 7 grasses responded similarly as we advanced from month to month in 1992, but both main effects (Table 2) and the month x species interaction were significant (P < 0.01) for 1993. In 1993, all 7 grasses exhibited a nearly linear or curvilinear decline of Zn as the seasons progressed (Fig. 7). Sandberg's bluegrass was the only forage to show a significant (P < 0.05) increase of Zn with the advent of fall precipitation in 1993. Despite these dynamics, none of the grasses sampled met the NRC (1996) required concentration of Zn for beef cattle forage (28.8 mg kg^{-1}) for any sampling period in either year. Fleming (1963) noted that zinc content varies considerably among components of grass plants and found leaf/stem/flower concentrations of 20, 15, and 36 mg kg^{-1}, respectively. Zinc deficiencies can cause parakeratosis (inflamed skin around nose and mouth), stiffness of joints, alopecia, breaks in skin around the hoof, and retarded growth. Deficiencies have been induced experimentally in calves (Miller and Miller 1960), and while no applied reports of Zn deficiencies have occurred in sheep or cattle (Maynard and Loosli 1969), Mayland et al. (1980) saw improved gains among calves supplemented with zinc in southern Idaho.

Manganese

Manganese concentrations varied significantly (P < 0.01) between years, and forages did not exhibit similar patterns as we advanced from month to month (Table 1) in either year. Variability among samples within months was high, however, and significant (P < 0.05) month to month changes in Mn concentration were difficult to establish within each species, especially in 1993 (Fig. 8).

With the exception of the beginning of the growing season (late-April), monthly Mn levels were generally higher for 1992 than for 1993. The NRC (1996) requirement for beef cattle was 38 mg kg^{-1}, and mean Mn content of forages over the 2 sampling seasons was 38.6 mg kg^{-1} (± 1.3). Only cheatgrass contained adequate concentrations of Mn early in the growing season, and it exceeded beef cattle requirements for all but the last months of both years. Other grasses, however, like bluebunch wheatgrass or bottlebrush squirreltail, consistently supported adequate levels of Mn late in the year, so cattle consuming a diverse diet could probably ingest sufficient Mn on a season long basis. Except for giant wildrye, which only contained adequate Mn levels in early May of both years, the other perennial bunchgrasses displayed more than required Mn levels from early to mid-June through early December in 1992. Sandberg's bluegrass, bluebunch wheatgrass, Idaho fescue, and Thurber's needlegrass were largely Mn deficient for beef

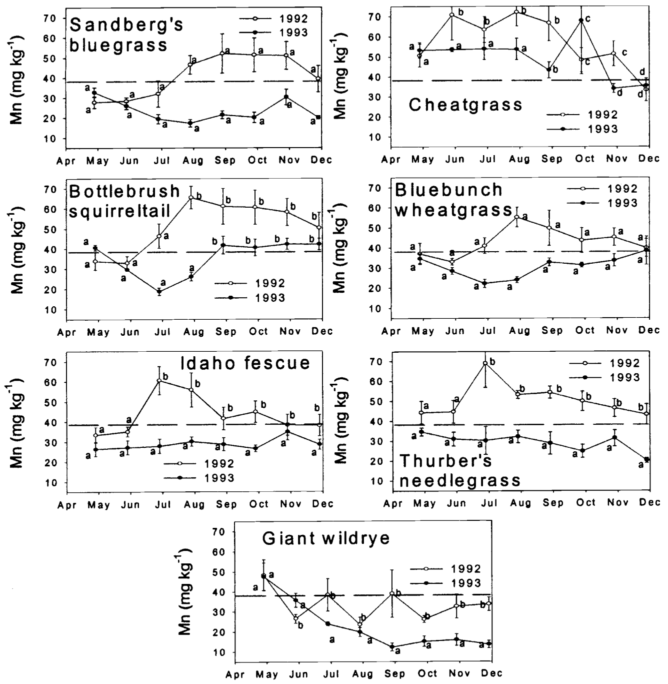

Fig. 8. Mean manganese content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes the required Mn content of forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly (P > 0.05) different. Fisher's protected LSD (P = 0.05) = 16.5 and 13.3 mg kg^{-1}, respectively, for 1992 and 1993.

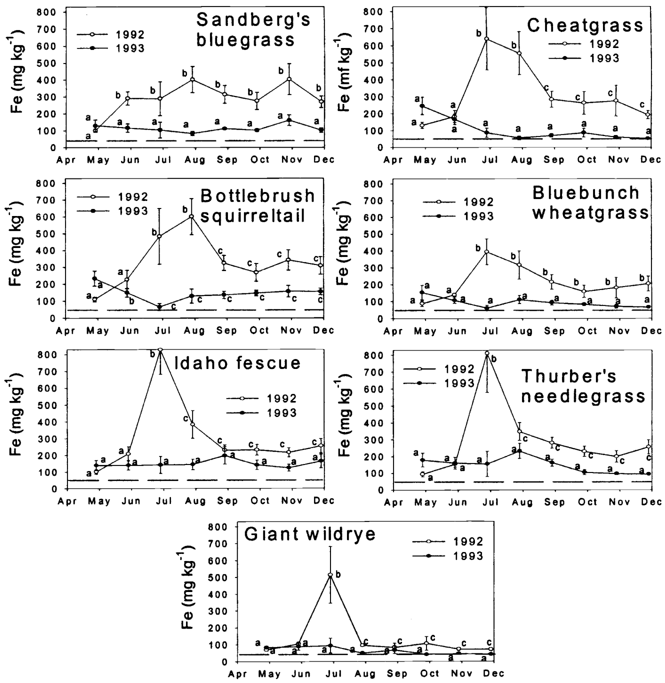

Fig. 9. Mean iron content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The dashed horizontal line denotes required Fe content of forages for a 454 kg cow. Adjacent monthly means within a year sharing a common letter are not significantly (P > 0.05) different. Fisher's protected LSD (P = 0.05) = 191.7 and 79.8 mg kg^{-1}, respectively, for 1992 and 1993.

cattle in the 1993 growing season and fall months. Giant wildrye cycled between being adequate and marginally deficient in 1992 and was largely deficient for the bulk of the 1993 sampling period.

Iron

With the exception of the year x species interaction (P = 0.186) in our initial analyses, (Table 1) most components of our analyses for Fe were significant (P < 0.01) (Table 2). Over the trial, mean Fe content of the grasses was 194.4 mg kg^{-1}, and each of the grasses exceeded or equaled beef cattle forage requirements of 48 mg kg^{-1} for all months sampled (Fig. 9). With the exception of the beginning of the growing season, Fe content of the grasses was higher (P < 0.01) in 1992 than in 1993. The 1992 sampling period also exhibited more seasonal dynamics within each grass than 1993 (Fig. 9), and we have some suspicion that rainfall and associated soil contamination of samples may have elevated Fe concentrations of our July 1992 period (Mayland and Sneva 1983). In 1993, the only significant (P < 0.05) month to month change in Fe concentration involved decreasing levels in bottlebrush squirreltail between late-April and late-June. It appears that above average June rainfall in 1992 stimulated Fe uptake (P < 0.05) by all of the grasses except Sandberg's bluegrass, while above average precipitation in July 1993 had no significant (P > 0.05) effect on Fe uptake.

Sodium

Sodium concentrations varied considerably among the grasses with substantial monthly differences between years (P < 0.01) (Table 1). While species and monthly differences (P < 0.05) occurred within years, all the grasses responded similarly (P > 0.13) as we advanced from month to month (Table 2 and Fig. 10) within each year. With the exception of the beginning of the growing season, monthly concentrations were typically higher for all the grasses in 1992 than in 1993. The NRC recommended sodium content for beef cattle forages was 672 mg kg^{-1}, and all of our forages were deficient throughout both years. Mean Na content of forages for the study was only 61.3 mg kg^{-1}. The highest Na content attained by any of the grasses was Sandberg's bluegrass in late-October of 1992, and even then, it averaged only 177 mg kg^{-1} (Fig. 10).

Among animals, Na is found primarily in extracellular fluids. In conjunction with K and Cl, it assists with maintaining osmotic pressure, acid-base equilibrium, nutrient passage into cells, and water metabolism in general (Maynard and Loosli 1969). Animals have considerable ability to conserve Na, but again that luxury is not available to lactating individuals (McDowell and Valle 2000) suffering from a lack of salt in the diet. Prolonged deficiencies cause loss of appetite, decreased growth or weight loss, unthrifty appearance and reduced milking (McDowell and Valle 2000), but supplemental salt can also stimulate weight gains (McDowell et al. 1984) among animals that are not showing signs of deficiencies.

Management implications

Cattle in the sagebrush/steppe typically derive 85 to 90% of their annual rangeland diet from grasses (Vavra and Sneva 1978, McInnis and Vavra 1987). Seasonally, spring/summer forbs may contribute as much as 6–9% of the diet, and shrubs may account for 12–15% of intake during fall and winter (McInnis and Vavra 1987). Given the preponderance of grasses in cattle diets, however, many of the patterns

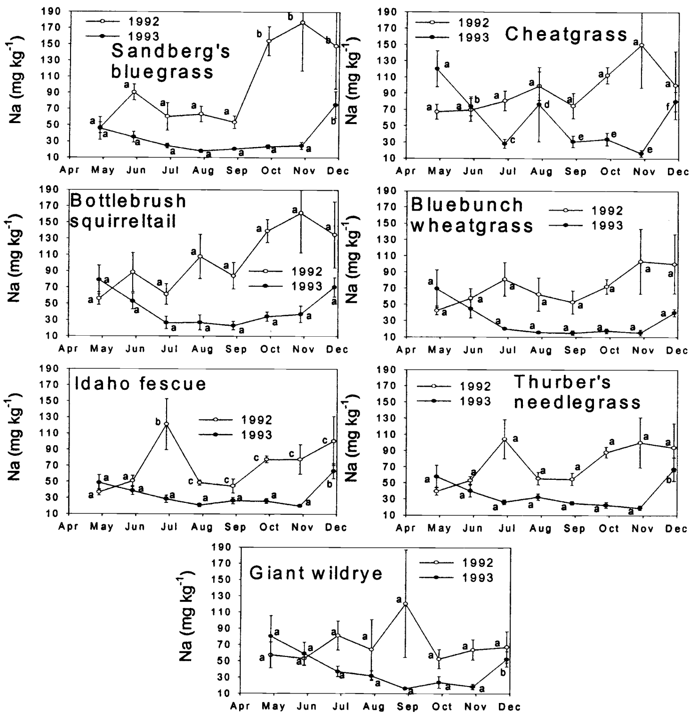

Fig. 10. Mean sodium content (±SE bars) of 7 grasses sampled over 8 months at 6 sites in the sagebrush steppe near Burns, Ore. in 1992 and 1993. The required sodium content of forages for a 454 kg cow is 672 mg kg^{-1}. Adjacent monthly means within a year sharing a common letter are not significantly ($P > 0.05$) different. Fisher's protected LSD ($P = 0.05$) = 61.5 and 30.8 mg kg^{-1}, respectively, for 1992 and 1993.

and generalizations from this study are especially relevant to beef cattle management and animal performance.

Of major interest were those minerals that occurred at deficient levels among grasses on a year around basis. These included Cu, Zn, and Na, and their deficiencies should most definitely be given some consideration by stockman (Figs. 6, 7, and 10). Seasonally deficient minerals included Ca, Mg, P, K, and Mn. Among the caespitose grasses, Ca and Mn were largely deficient for cattle early in the growing season with levels increasing as the grasses advanced into summer (Figs. 2 and 8). Magnesium patterns were less generalized (Fig. 4) because some grasses displayed increasing concentrations as the seasons progressed (giant wildrye and bottlebrush squirreltail), some remained relatively stable through the seasons (bluebunch wheatgrass and Thurber's needlegrass), and others declined (Sandberg's bluegrass and cheatgrass). Phosphorus and K levels were typically adequate early in the growing season and declined to deficient levels by July and August, respectively (Figs. 4 and 5). Iron was of no concern, because levels were more than adequate among all the grasses for all periods sampled. However, high levels of Fe could potentially lower Cu availability and exasperate management problems associated with copper deficiencies.

Also of interest was the year to year dynamics that occurred among minerals within a species. With the exception of a few early and late season reversals, a gross generalization was that mineral concentrations were higher during the 1992 growing season than for 1993. We did not quantify leaf/stem/flower ratios of our samples, but our field notes clearly indicated that very few grasses completed the reproductive phases of phenology during the 1992 growing season. Abundant early moisture in 1993, however, allowed great numbers of tillers to fully complete their reproductive efforts before going dormant. That being the case, the summer/fall 1992 samples were largely vegetative in nature, while the 1993 samples contained a wealth of reproductive stems. These reproductive stems do add biomass, as 1993 standing crop was more than twice that of 1992 (Ganskopp and Bohnert 2001), but they dilute nutritive value (Ganskopp et al. 1992, Mayland and Shewmaker 1997), because they are largely generated for structural support of reproductive parts.

Angell et al. (1990) noted significant disparities in crude protein content of crested wheatgrass at equivalent dates and stages of morphological development among years, and our data also exhibit some substantial disparities within months and between years for each species. Calcium, Mg, and Mn concentrations fluctuated greatly between years, and indeed some grasses supported deficient levels for 1 sampling season and more than adequate levels for beef cattle during a second. The clearest and most radical example was Thurber's needlegrass with Ca and Mn between 1992 and 1993 (Figs. 2 and 8). Both minerals were more than adequate in 1992 and at deficient concentrations for all of the 1993 sampling period. Other grasses like bottlebrush squirreltail, bluebunch wheatgrass, and Idaho fescue approached this same pattern, but there were periods in both years when they contained deficient concentrations.

Indeed plant mineral dynamics and animal mineral nutrition are complex issues, and our most prominent forages are clearly deficient for one or more minerals for much of the year. A few items, however, should be mentioned to illustrate that nutritive value, or perhaps more correctly, range quality, may be better than indicated by our data. First, we should point out that our analyzed materials included whole plant samples taken above a 2.5-cm stubble. Large herbivores typically harvest diets of higher quality than hand-compounded rations or whole-plant samples by selecting specific plant parts or portions (Kiesling et al. 1969, McInnis and Vavra 1987, Cruz and Ganskopp 1998). That being the case, adequate mineral concentrations in cattle diets probably extend for longer periods of time than suggested by our data. On the downside, however, the actual availability of forage minerals to ruminants also fluctuates seasonally (Peeler 1972).

Second, cattle do forage from a variety of available forages. Early in the growing season cattle may select up to 80% of their diet from a single grass, but their diets become more diverse as forages mature (Cruz and Ganskopp 1998). Thus a substantial portion of their intake is derived from other sources, and there may be forbs and shrubs available that can also help rectify deitary deficiencies. Clearly, our data show a diversity of grasses can extend the period of adequate nutrition, and some of the less desirable grasses like cheatgrass and Sandberg's bluegrass do furnish excellent early forage and respond to small amounts of precipitation with nutritious vegetative growth late in the season (Figs. 2, 3, and 8).

Third, there may be natural licks or mineral sources in the area. In some of our intensive, grazing behavior studies at the Northern Great Basin Experimental Range (Cruz and Ganskopp 1998, Ganskopp et al. 1997) we observed instances where cattle ceased grazing and licked bare soil for up to 1 minute. The nutritional value of these events, however, were not quantified. Lastly, livestock have many mechanisms for either conserving, recycling, mobilizing or buffering mineral or nutrient balances within their systems, and these mechanisms allow them to endure short term deficiencies without ill effects (Maynard and Loosli 1969). Again though, lactating animals can not avail themselves of many of these mechanisms (Underwood 1981) when grazing deficient forages.

Addressing a variety of nutritional deficiencies is a vexing problem for producers. In intensively managed pasture, many mineral deficiencies can be rectified by treating the land with a required element or altering pH of the soil to enhance mineral availability for growing forages (MacPherson 2000). Other options include either oral treatments or injections for stock (Allen and Moore 1983). With large-scale feedlot situations, frequent ration sampling and custom supplement formulations may be mixed on even a daily basis to accommodate the dynamics of variable quality in feed supplies.

In most extensive rangeland systems, however, these solutions are economically and/or logistically impossible, and the only recourse is to supply free-access supplements in either block or loose form. MacPherson (2000) suggests these formulations have greatest efficacy if positioned near watering points with 1 station for every 25–40 cows. Conventional wisdom, however, suggest though that rangeland managers should try to disperse their cattle uniformly across pastures by positioning supplements some distance from the areas where their animals typically concentrate (Ares 1953, Bailey and Welling 1999) .

Given the logistical demands of ascertaining forage nutritive value and supplement delivery in extensive pastures, ranchers for the most part can not respond to seasonal nutritional dynamics of their forages. Most likely, the best approach is to use a supplement formulation with the ability to rectify all known year-round and potential seasonal deficiencies of their forages. Based on our findings, mineral supplementation is probably more of an issue during what we perceive as good forage years than when plant growth and development are arrested by drought. McDowell and Valle (2000) list several desirable characteristics of mineral supplement formulations and also warn that mineral excesses are capable of inducing other deficiencies. When formulating mineral supplements for cattle pasturing in the northern sagebrush steppe, we recommend that 8 of the 9 minerals evaluated in this study be added to the mix. These included Ca, Mg, Cu, P, K, Zn, Mn, and Na. Adequate concentrations of iron were available on a year-round basis in all the grasses studied.

Conclusions

Year-to-year, month-to-month, and species specific patterns of mineral concentrations were quite variable among the 7 northern Great Basin rangeland grasses sampled. Minerals that were deficient on a year-round basis included Cu, Zn, and Na, and these should of course be additives to any rangeland supplement formulation for beef cattle. Minerals which were seasonally deficient, and in some instances, deficient though out an entire growing season were: Ca, Mg, P, K, and Mn. Month to month patterns among these found low levels of Ca, Mg, and Mn early in the growing season with concentrations increasing as forages matured and concentrations declining as plants became weathered and dormant. Phosphorus and K levels were elevated early in the growing season and declined to deficient levels by early July or August. Iron was the only mineral assayed with adequate year-round concentrations in all forages. Contrary to intuitive thinking, mineral concentrations were generally higher among the grasses when soil moisture levels were restricted and plants could not fully advance though their reproductive stages of growth. Shallow rooted grasses like Sandberg's bluegrass, bottlebrush squirreltail, or the winter annual cheatgrass can quickly respond to mid-summer or fall precipitation and furnish additional high quality herbage. Cattle can possibly extend their periods of adequate mineral nutrition by selectively grazing among mixtures of these grasses. We suggest, however, that a mineral supplement be available season-long on northern Great Basin rangelands and that the formulation include at least Ca, Mg, P, K, Cu, Zn, Mn, and Na in available forms and proper ratios.

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56: 185-192 March 2003

Vegetation dynamics from annually burning tallgrass prairie in different seasons

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Abstract

Traditional perception of how tallgrass prairie responds to fire at times other than late spring is either anecdotal or extrapolated from studies that lack spatial or temporal variability. Therefore, we evaluated patterns of change in vegetation cover, species richness, diversity, and aboveground biomass production on 2 different topographic positions from ungrazed watersheds that were burned annually for 8 years in either autumn (November), winter (February), or spring (April). Topoedaphic factors influenced the response patterns of some species to seasonal fire, although differences were primarily in the rate of change. Annual burning in autumn and winter produced similar trends through time for most species. Big bluestem (*Andropogon gerardii* Vitman) cover increased with all burn regimes, whereas indiangrass [*Sorghastrum nutans* (L.) Nash] increased only with spring burning. Repeated autumn and winter burning eventually increased perennial forb cover, with the largest increases occurring in heath aster [*Symphyotrichum ericoides* (L.) Nesom], aromatic aster [*S. oblognifolium* (Nutt.) Nesom], tall goldenrod (*Solidago canadensis* L.), and legumes. Species richness increased (P < 0.001) through time with spring and winter burning, but was similar among all burn treatments after 8 years of annual fire. Average grass and forb biomass did not differ among burn seasons on either topographic position, although interannual biomass production fluctuated inconsistently with time of burn. Our findings contrast with many of the conventional views of how tallgrass prairie vegetation responds to seasonal fire and challenges traditional recommendations that burning should only occur in late spring.

Key Words: burn season, fire ecology, grassland vegetation

Resumen

La percepción tradicional de como la pradera de zacates altos responde al fuego en tiempos distintos a fines de primavera es anecdótica o extrapolada de estudios que carecen de variabilidad espacial y temporal. Por lo tanto, nosotros evaluamos los patrones de cambio en la cobertura vegetal, riqueza de especies, diversidad y producción de biomasa en 2 posiciones topográficas diferentes de cuencas hidrológicas sin apacentamiento que fueron quemadas anualmente por 8 años tanto en otoño (Noviembre), invierno (Febrero) o primavera (Abril). Los factores topoedáficos influenciaron los patrones de respuesta de algunas especies al fuego estacional, aunque las diferencias fueron principalmente en la tasa de cambio. La quema anual en otoño e invierno produjo tendencias similares a través del tiempo para la mayoría de las especies. La cobertura de "Big bluestem" (*Andropogon gerardii* Vitman) se incrementó con todos los regímenes de quema mientras que la del "Indiangrass" [*Sorghastrum nutans* (L.) Nash] se incrementó solo con la quema de primavera.. Las quemas repetidas en otoño e invierno eventualmente aumentaron la cobertura de hierbas perennes y el mayor aumento ocurrió en "Heath aster" [*Symphyotrichum ericoides* (L.) Nesom], "Aromatic aster" [*S. oblognifolium* (Nutt.) Nesom], "Tall goldenrod" (*Solidago canadensis* L.) y leguminosas. La riqueza de especies se incrementó (P < 0.001) a través del tiempo con las quemas de primavera e invierno, pero después de 8 años de quemas anuales fue similar en todos los tratamientos de quema. La biomasa promedio de zacates y hierbas no difirió entre las épocas de quema en cualquiera de las posiciones topográficas, aunque la producción interanual de biomasa fluctuó inconsistentemente con el tiempo de quema. Nuestros hallazgos contrastan con muchos de los puntos de vista convencionales de como la vegetación de las praderas de zacates altos responde al fuego estacional y reta a las recomendaciones tradicionales de que la quema debe ocurrir solo a fines de primavera.

Fire is an integral component of prairie development (Axelrod 1985), and for more than 7,000 years vegetation patterns have been influenced by anthropogenic burning practices (Sauer 1944, Stewart 1951, Woodcock and Wells 1994, Kimmerer and Lake 2001). Although presettlement prairie fires potentially could occur at any time of the year (Bragg 1982), intentional burning in autumn and late winter was a frequent ritual of most native American tribes (Catlin 1973, Pyne 1982, McClain and Elzinga 1994). Prairie fires were suppressed during European settlement, and accidental or lightning-caused wildfires were the primary source of burning (Hoy 1989, McClain and Elzinga 1994). After the influx of transient cattle to the Kansas Flint Hills in the late 1800's, however, the incentive for prairie burning renewed and pastures were ignited annually in February or March to improve livestock gains (Kollmorgen and Simonett 1965, Isern 1985). Traditional burn season shifted gradually to mid- or late-April,

Earlier drafts of this manuscript were improved by comments from David Hartnett and John Blair. We also thank Amanda Kuhl and the LTER clipping crew for the biomass collections. Konza Prairie Biological Station is a preserve of The Nature Conservancy managed by the Division of Biology at Kansas State University. The National Science Foundation Long-Term Ecological Research Program and the Kansas Agricultural Experiment Station provided support for this project. This paper is contribution No. 02-263-J from the Kansas Agricultural Experiment Station.
Manuscript accepted 2 Jul. 02.

because fire at that time favored the warm-season perennial grasses that are the mainstay of livestock grazing (McMurphy and Anderson 1965, Anderson et al. 1970). In addition, burning Kansas tallgrass prairie at times other than late spring has been staunchly discouraged because of reputed adverse effects on vegetation composition and productivity (Hanks and Anderson 1957, Anderson 1961, 1965, McMurphy and Anderson 1963, 1965, Owensby and Anderson 1967, Anderson et al. 1970).

The impetus of fire research in tallgrass prairie has focused on the vegetation responses imposed by fire frequency, with the burns occurring in April (Abrams and Hulbert 1987, Gibson and Hulbert 1987, Gibson 1988, Collins 1992). Perceptions of how tallgrass prairie responds to autumn or winter fires are derived either from small plots (Aldous 1934, McMurphy and Anderson 1963, 1965, Bragg 1982, Lovell et al. 1982, Towne and Owensby 1984), or from single burn events (Penfound and Kelting 1950, Kelting 1957, Adams and Anderson 1978, Adams et al. 1982). Topographic position, soil texture, and climatic factors, however, can affect how plants respond to fire (Abrams and Hulbert 1987, Gibson and Hulbert 1987), and documentation of spatial and temporal trends from repeated seasonal burning is lacking. Additionally, diversity indices and the response of most subdominant species to seasonal fire are anecdotal or speculative. Understanding the effects of seasonal burning on the dynamics of tallgrass prairie plants is important in formulating rational management, and conventional generalizations of how most species respond to season of fire may be misleading (Engle and Bidwell 2001). Thus, our objectives were to assess vegetation trends from an ongoing long-term study of annual burning in different seasons. Specific questions considered were: (1) What species are differentially affected by repeated autumn, winter, and spring fire, and does their response vary between topoedaphic sites? (2) How does species richness and diversity change in response to annual burning in different seasons? and (3) Are the purported adverse effects on biomass production from autumn and winter burning consistent across time and topographic positions?

Materials and Methods

Study Area

The study was conducted on Konza Prairie Biological Station, a 3,487-ha tallgrass prairie located in the Flint Hills of northeastern Kansas (39°05' N, 96°35' W). This site is the largest tract of tallgrass prairie in the United States that is specifically managed for ecological research. To study how fire affects the structure and function of grassland vegetation, Konza Prairie is parceled into 52 watersheds that provide large replicated experimental units subjected to different fire regimes. Vegetation is typical of native tallgrass prairie and is dominated by warm-season perennial grasses, primarily big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], and little bluestem [*Schizachyrium scoparium* (Michx.) Nash]. Forb species are widespread and constitute more than 75% of the species richness (Towne 2002).

The climate for the area is characterized by hot summers, cold winters, and moderately strong surface winds. Annual precipitation averages 859 mm, with 75% of this occurring in the April to September growing season. Between 1994 and 2001, annual precipitation exceeded the long term average on 4 occasions, although rainfall during the growing season was above average in only 3 years (Fig. 1). The average frost-free season lasts 180 days.

Six watersheds that have not been grazed by cattle for more than 30 years were selected for a long-term seasonal burning study. The watersheds ranged in size from 11 to 39 ha and had been burned previously every 3 or 4 years in the spring

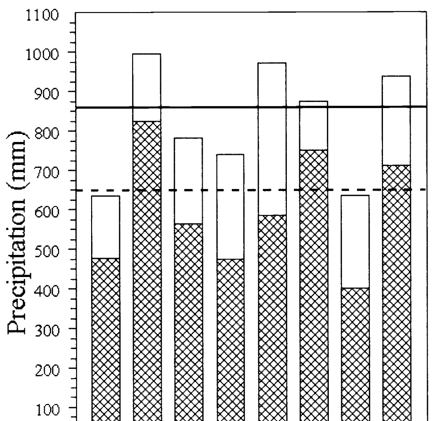

Fig. 1. Total annual precipitation and growing season (Apr–Sep) precipitation (lower hatched bar) for the years 1994-2001 at Konza Prairie. The solid horizontal line represents the 30 year annual precipitation mean. The dashed horizontal line represents the 30 year growing season precipitation mean.

since 1972. Topographically, the watersheds are comprised of upland plateaus, rocky hillsides, and fertile lowlands. The upland topographic positions are relatively shallow, silty clay loams overlying limestone and shale layers (Udic Argiustolls, Florence series), whereas the lowland positions are deeper colluvial and alluvial deposits (Pachic Argiustolls, Tully series). Seasonal burning began in November 1993, when 2 watersheds were burned for the autumn treatment. Subsequent fire treatments included 2 watersheds that were burned in February 1994 and 2 in April 1994 for the winter and spring treatments, respectively. The same 2 watersheds were burned in the same season throughout the study. Average burn dates for the 8-year period were 26 November, 17 February, and 24 April. All burns were conducted under conditions of moderate wind speed and humidity, producing relatively intense head fires.

Data Collection

Species composition sampling began in 1994 after four, 50-m long transects, each with 5 permanent plots, were established on both upland and lowland topographic positions in all watersheds (n = 20 plots for each topographic position). The canopy cover of every species in a 10-m^2 circular area around each plot was estimated and assigned to a percentage category (Bailey and Poulton 1968). Cover of individual species was determined by averaging the midpoint of the cover categories (i.e., 0.5, 3, 15, 37.5, 62.5, 85, and 97.5%) across the 20 plots for each topographic position. We also calculated frequency of occurrence (the proportion of plots where an individual species occurred) as an alternative indication of how species respond to seasonal fire. All plots were surveyed each year in June and August.

Aboveground biomass production was measured at the end of each growing season by clipping 5 randomly selected quadrats (0.1 m^2) adjacent to each plant composition transect (n = 20 plots per topographic position). Vegetation in the plots was clipped at ground level, separated into graminoid, forb, and woody components, oven-dried at 60°C, and weighed.

Data Analysis

A total of 148 species were encountered in this study, but only those species with > 2% mean canopy cover in any year or treatment were analyzed individually. Canopy cover of individual species and the summed cover of species in similar taxonomic and life-form groups (e.g., sedges, legumes, annual forbs, and woody species) were arcsine square-root transformed and analyzed as a split-split plot over time. The full model contained terms for burn season, topographic position, year, and their interactions. To evaluate patterns of change through time from seasonal burning, we used the annual deviation from the mean year value for the 8-year study period as a linear covariate and the deviation squared as a quadratic covariate. We initially fit a full covariance model to each independent variable and the nonsignificant ($P > 0.05$) effects were then deleted systematically. Inferences regarding trends through time were based on the respective regression coefficients. If a species response to season of fire differed between topographic positions, the regression slopes were tested for each site using appropriate contrasts. Otherwise, the response was combined across topographic positions and the slopes for each burn season compared. Linear and quadratic response curves were fitted using least square regression.

Aboveground biomass was analyzed as a split-split plot with burn season as the whole plot factor, topographic position as the subplot factor, and year as the sub-subplot factor. The effect of burn season was tested using the variation between replicate watersheds (nested within burn seasons) as the whole plot error term; topographic effects were tested using the topographic position x watershed (nested within burn season) mean square as the subplot error term; and year effects were tested with the residual mean square.

Species richness (the cumulative number of plant species detected in the 20 plots for each topographic position) and the Shannon diversity index ($H' = \sum p_i \times \ln p_i$, where p_i is the canopy cover of each species) were square-root transformed and analyzed using the split-split plot over time covariance model. Frequency values were arcsine square-root transformed and analyzed using the split-split plot model, with burn season as the whole-plot factor and topographic position and year as the split factors. We used SAS procedures (SAS Institute 1999) to analyze the data, with 0.05 as the probability level to establish statistical significance.

Results and Discussion

Topoedaphic factors influenced the response patterns of some species to repeated seasonal burning, although differences were primarily from variation in the rate of change. In general, most species that responded to time of burning followed gradual curvilinear shifts through time. The quadratic downward trend exhibited by some species indicated sensitivity to fire, after which the population maintained its presence in the community at a lower level. In contrast, the concave temporal trend of some species indicated a negative short-term impact to fire, followed by a period where the species recovered to pre-existing levels. The canopy cover of most species, however, remained stable through time, suggesting tolerance to annual burning in any season.

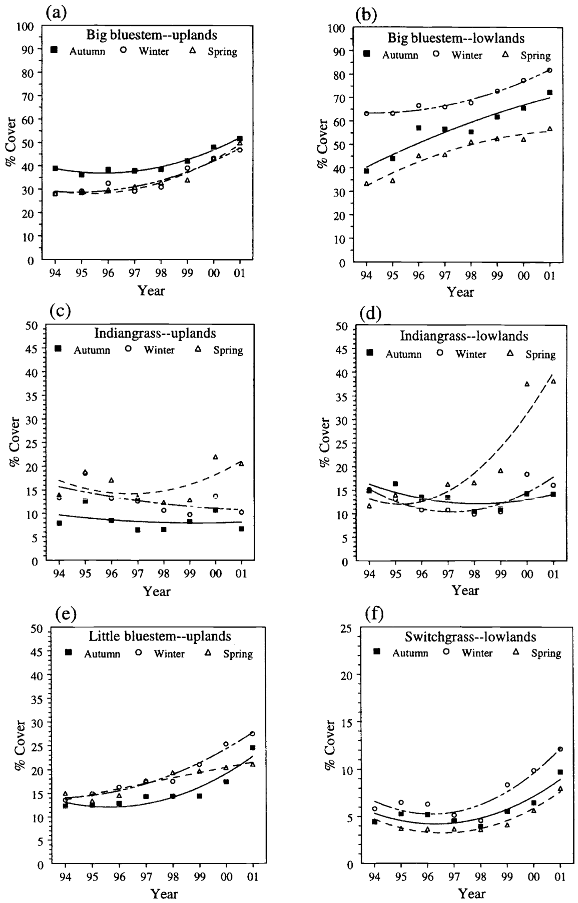

Fig. 2. Canopy cover changes through time in response to annual autumn, winter, and spring burning: (a, b) big bluestem on upland and lowland topographic locations, (c, d) indiangrass on upland and lowland topographic locations, (e) little bluestem on upland sites, and (d) switchgrass on lowland sites.

Warm-season Grasses

Burning in autumn and winter produced similar response patterns through time in all warm-season grass species. Big bluestem cover increased in response to annual burning in any season, although the changes through time were smaller on upland topographic positions (Fig. 2a) than on lowland positions (Fig. 2b). Indiangrass increased only with spring burning, and exhibited the largest response of any warm-season grass to fire. However, it required 7 consecutive burns before the upturn, with the greatest increase occurring on lowland topographic sites (Fig. 2c, 2d). Little bluestem cover increased on upland locations with autumn and winter burning, but did not change ($P = 0.13$) in response to spring burning (Fig. 2e). On lowland sites, little bluestem cover remained stable through time with all burn treatments (Table 1). Switchgrass (*Panicum virgatum* L.) increased in response to fire in any season on lowland sites (Fig. 2f); but on upland sites, switchgrass cover did not change significantly through time with any burn treatment (Table 1).

The collective canopy cover of all warm-season grasses increased from burning in any season, although the rate of change differed between topographic positions. On upland sites, the increases through time were similar for all burn sea-

Table 1. **Average percent cover of graminoid species after 8 years of annual burning in different seasons on upland and lowland topographic positions. A positive superscript indicates cover increased (P < 0.05) from 1994. A negative superscript indicates cover declined significantly from 1994.**

Species	Uplands			Lowlands		
	Autumn	Winter	Spring	Autumn	Winter	Spring
	----------	(%)	----------	----------	(%)	----------
Andropogon gerardii	51.7^{+}	46.9^{+}	49.9^{+}	72.4^{+}	81.9^{+}	57.0^{+}
Bouteloua curtipendula	3.5	2.6	3.0^{-}	0.1	0.2	0.2^{-}
Panicum virgatum	1.8	2.3	4.8	9.7^{+}	12.1^{+}	8.0^{+}
Schizachyrium scoparium	24.6^{+}	27.5^{+}	21.1	13.4	2.5	14.4
Sorghastrum nutans	6.7	10.2	20.6^{+}	14.2	16.1	38.2^{+}
Sporobolus compositus	0.8^{-}	2.0^{-}	0.9^{-}	4.8^{-}	2.5^{-}	0.9^{-}
Sporobolus heterolepis	3.7^{+}	1.7^{+}	1.7	0.1	0.6	1.1
All warm-season grasses	93.1^{+}	93.7^{+}	102.4^{+}	114.7^{+}	115.9^{+}	120.7^{+}
Carex spp.	17.5^{+}	17.1^{+}	1.4^{-}	15.8^{+}	11.6^{+}	4.9^{-}
Dichanthelium oligosanthes	2.9	8.3	1.0^{-}	1.4	1.2	0.7^{-}
Koeleria macrantha	9.3^{+}	2.7	0.2	< 0.1	< 0.1	< 0.1
Poa pratensis	0.1^{-}	0.1^{-}	0.1^{-}	0.3^{-}	0.4^{-}	0.1^{-}
All cool-season graminoids	30.2^{+}	28.3^{+}	2.6^{-}	17.9	13.3	6.8^{-}

sons (Fig. 3a); but on lowland sites, spring burning produced the greatest increase in warm-season grass cover (Fig. 3b). Not all warm-season grass species, however, tolerated or benefitted from annual burning. Tall dropseed [*Sporobolus compositus* (Poir.) Merr.] decreased in response to fire in any season (Table 1). Cover of side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.] also was reduced with spring burning, but not from autumn or winter burning (Table 1).

Cool-season Graminoids

Prairie junegrass [*Koeleria macrantha* (Ledeb.) Schult.], a species predominant on upland sites, increased linearly in response to autumn burning, but remained stable through time with winter and spring burning (Fig. 3c). All other cool-season graminoids declined significantly with repeated spring burning, whereas Kentucky bluegrass (*Poa pratensis* L.) was the only cool-season species that declined in response to autumn and winter burning (Table 1). On upland sites, Scribner's panicum [*Dichanthelium

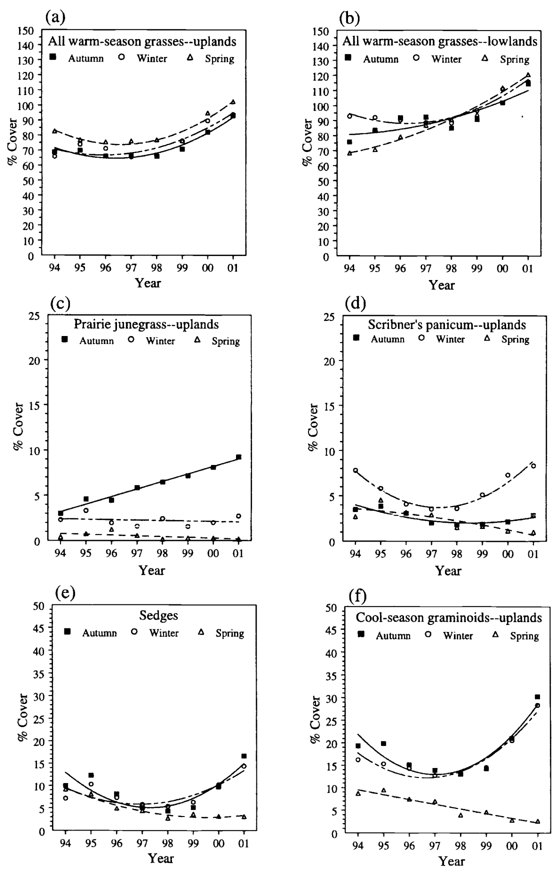

Fig. 3. Canopy cover changes through time in response to annual autumn, winter, and spring burning: (a, b) total cover of all warm-season grass species on upland and lowland topographic locations, (c) prairie junegrass on upland sites, (d) Scribner's panicum on upland sites, (e) sedges for both topographic sites combined, and (f) total cover of all cool-season graminoids on upland sites.

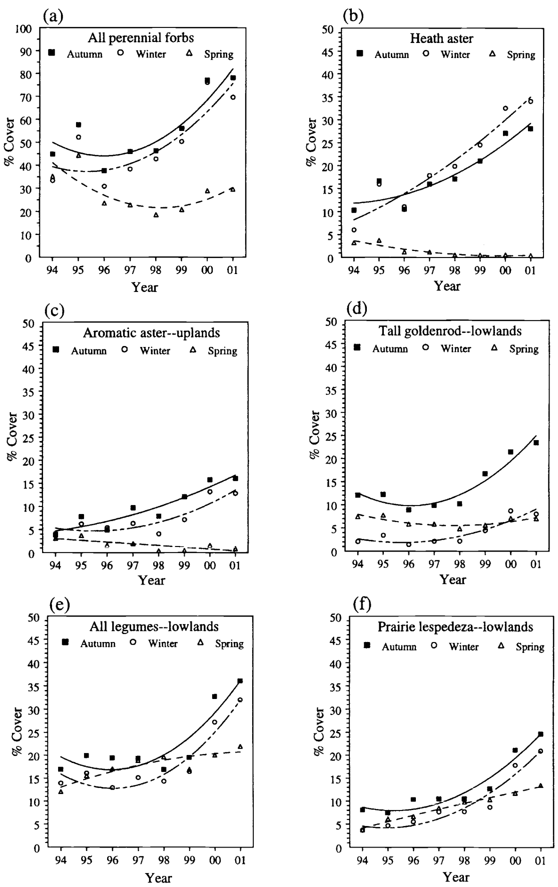

Fig. 4. Canopy cover changes through time in response to annual autumn, winter, and spring burning for various perennial forbs on different topographic positions: (a) total cover of all perennial forbs for both topographic sites combined, (b) heath aster for both topographic sites combined, (c) aromatic aster on upland sites, (d) tall goldenrod on lowland sites, (d) total cover of all legume species on lowland sites, and (f) prairie lespedeza on lowland sites.

Table 2. Average percent cover of various forb species after 8 years of annual burning in different seasons on upland and lowland topographic positions. A positive superscript indicates cover increased (P < 0.05) from 1994. A negative superscript indicates cover declined significantly from 1994.

	Uplands			Lowlands		
Species	Autumn	Winter	Spring	Autumn	Winter	Spring
	---------- (%) ----------			---------- (%) ----------		
Ambrosia psilostachya	2.0	1.3	0.7	1.4	1.5	1.6
Artemisia ludoviciana	0.2^{-}	0.7^{-}	< 0.1^{-}	1.4	0.3	< 0.1^{-}
Brickellia eupatorioides	0.8	1.0	0.8^{-}	0.5	0.1	0.5
Physalis pumila	0.5	0.4^{-}	0.5	0.6^{-}	0.5^{-}	0.7^{-}
Ruellia humilis	0.3^{-}	0.4^{-}	0.4	0.5^{-}	0.4^{-}	2.3
Salvia azurea	5.8^{+}	4.0	5.7	0.1	< 0.1	0
Solidago canadensis	0	0	0	23.5^{+}	8.0^{+}	7.0
Solidago missouriensis	0.3	0.4^{-}	0.4^{-}	0.4	1.8	3.0
Symphyotrichum ericoides	17.9^{+}	23.1^{+}	0.5^{-}	38.3^{+}	44.9^{+}	0.4^{-}
Symphyotrichum oblongifolium	16.0^{+}	12.8^{+}	0.9^{-}	0	0	0
All perennial forbs	51.9^{+}	51.8^{+}	16.1	104.4^{+}	87.4^{+}	43.1
Amorpha canescens	2.8	0.4	3.3	3.8	4.9	5.5
Dalea canadia	0.2	0.7	0.1	2.0^{+}	1.7	0.8
Lespedeza capitata	0.2	0.7	0.1	2.3^{+}	2.3	1.3
Lespedeza violaceae	< 0.1	< 0.1	< 0.1	24.6^{+}	20.9^{+}	13.4^{+}
All legume species	7.3	5.4	6.3	36.1+	32.0^{+}	21.9^{+}
All annual forbs	0.2	0.1	0.2	0.3	0.2	0.7
All woody species	0.2	0.2	0.7	0.8	2.2	1.6

oligosanthes (Nash) Gould], the most common cool-season grass on Konza Prairie, declined and then recovered to beginning levels in response to winter burning (Fig. 3d); but on lowland sites, the temporal patterns remained stable with both winter and autumn burning (Table 1). Sedges [primarily *Carex inops* Bailey, *C. meadii* Dewey, *C. brevior* (Dewey) Mack., and *Cyperus lupulinus* (Spreng.) Marcks] also declined initially in response to both autumn and winter burning before diverging upward and attaining the highest cover values after 8 years of fire (Fig. 3e). The collective cover of all cool-season graminoids followed concave patterns through time with autumn and winter burning. Although the trends were similar on both topographic positions, cool-season graminoid cover eventually surpassed initial values on upland sites (Fig. 3f), but only recovered to the original levels on lowland sites (Table 1). The transitory decline of most cool-season graminoid species in response to autumn and winter burning coincided with 3 consecutive years of below normal precipitation during the growing season, suggesting that moisture availability may be crucial in mediating their response patterns to seasonal fire.

Perennial Forbs

The combined cover of all perennial forbs responded with similar curvilinear upward trends in response to autumn and winter burning, but did not change through time with spring burning (Fig. 4a). Species that were primarily responsible for the increase in forb cover from repeated autumn and winter burning were heath aster [*Symphyotrichum ericoides* (L.) Nesom], aromatic aster [*S. oblongifolium* (Nutt.) Nesom], and tall goldenrod (*Solidago canadensis* L.) (Figs. 4b-4d). Western ragweed (*Ambrosia psilostachya* DC), a dominant forb in tallgrass prairie, was not affected (P > 0.10) by time of burning on either topographic position (Table 2). However, dynamic interannual fluctuations in western ragweed cover suggest that factors other than season of burn influenced temporal patterns. Although burning in autumn or early-spring will putatively increase forbs or "weedy" species (Anderson 1961, Anderson et al. 1970, Schwegman and McClain 1985), it required repeated burning in autumn or winter before forb canopy cover eventually increased.

Total legume cover increased on lowland sites in response to burning in any season, but the greatest changes through time occurred with autumn and winter burning (Fig. 4e). Prairie lespedeza [*Lespedeza violaceae* (L.) Pers.], a species occurring predominantly on lowland sites, exhibited the most prominent increase of all legumes to annual burning, and was the only forb species that increased with spring burning (Fig. 4f). Cover of leadplant (*Amorpha canescens* Pursh), the

Table 3. Average percent frequency of species that changed significantly after 8 years of annual burning in different seasons on upland and lowland topographic positions (10-m^2 plots; n = 40). A positive superscript indicates the frequency of occurrence increased (P < 0.05) from 1994. A negative superscript indicates the frequency declined significantly from 1994.

	Uplands			Lowlands		
Species	Autumn	Winter	Spring	Autumn	Winter	Spring
Grasses:	---------- (%) ----------			---------- (%) ----------		
Bouteloua curtipendula	77.5	97.5^{+}	100	17.5	37.5^{+}	30.0
Bouteloua gracilis	22.5^{+}	30.0	32.5^{+}	0	0	0
Dichanthelium acuminatum	5.0	0	7.5	27.5	15.0^{+}	42.5^{+}
Dichanthelium oligosanthes	100	100	100^{+}	90.0^{+}	92.5	100^{+}
Eragrostis spectabilis	7.5	30.0	27.5	7.5	7.5	75.0^{+}
Schizachyrium scoparium	87.5	95.0	95.0	92.5^{+}	72.5	95.0^{+}
Sporobolus compositus	85.0	95.0^{+}	75.0	97.5	97.5^{+}	90.0
Poa pratensis	15.0^{-}	32.5^{-}	15.0^{-}	62.5^{-}	45.0	22.5^{-}
Forbs:						
Asclepias verticillata	32.5	42.5	27.5	25.0	15.0^{-}	77.5^{+}
Asclepias viridis	20.0^{-}	35.0	35.0	37.5	22.5^{-}	70.0^{+}
Artemisia ludoviciana	35.0	67.5	15.0^{-}	40.0	32.5	7.5^{-}
Cirsium altissimum	2.5	0	0	35.0^{-}	20.0	15.0^{-}
Dalea candida	27.5^{+}	37.5^{+}	22.5^{+}	75.0^{+}	80.0^{+}	72.5^{+}
Dalea purpurea	65.0^{+}	52.5^{+}	70.0^{+}	15.0	35.0^{+}	0
Lespedeza capitata	32.5^{+}	32.5^{+}	17.5	67.5^{+}	60.0^{+}	67.5^{+}
Lespedeza violacea	2.5	2.5	2.5	82.5^{+}	85.0^{+}	57.5^{+}
Oxalis stricta	15.0	2.5	0^{-}	5.0	2.5	42.5
Oxalis violacea	0	2.5	2.5	82.5	52.5	80.0^{+}
Physalis pumila	47.5	42.5	52.5^{+}	70.0^{+}	85.0	92.5^{+}
Ruellia humilis	67.5^{+}	72.5^{+}	65.0	82.5	75.0	87.5
Solidago canadensis	0	0	0	55.0	55.0^{+}	52.5
Solidago missouriensis	27.5	47.5	37.5	37.5	35.0	52.5^{+}
Vernonia baldwinii	55.0	67.5	40.0	67.5	70.0^{+}	60.0

most common legume species on Konza Prairie, did not change significantly on either topographic position after 8 years of burning in any season (Table 2). Densities of many legume species are higher in tallgrass prairie burned annually in the spring than in prairie that is not burned (Towne and Knapp 1996). Trends in canopy cover, however, suggest that most legume species tolerate annual spring fire rather than benefit directly from it.

Annual Species

Annual forb species were too sparse to analyze individually, but the combined canopy cover of all annual forbs did not change through time with any burn treatment (Table 2). Collectively, annual forbs averaged 0.6% cover the first 2 years of burning, after which levels dropped and stabilized in all burn treatments. In contrast, extremely low levels of 2 annual grass species [common witchgrass (*Panicum capillare* L.) and little barley (*Hordeum pusillum* Nutt.)] were detected in the first 2 years of the study, but subsequently disappeared and never reappeared in any burn treatment.

Annual plants are potentially susceptible to fire, but some forb species [e.g., daisy fleabane (*Erigeron strigosus* Muhl. ex Willd.) and grooved flax (*Linum sulcatum* Riddell)] persisted under all burn regimes. A few annual species [e.g., annual ragweed (*Ambrosia artemisiifolia* L.), snow-on-the-mountain (*Euphorbia marginata* Pursh), common pepperweed (*Lepidium densiflorum* Schrad.), and smooth-seed wildbean (*Strophostyles leiosperma* (Torr. & A. Gray) Piper)] appeared sporadically in some years. However, most other annual forb species [e.g., rough false-penny-royal (*Hedeoma hispida* Pursh), prickly lettuce (*Lactuca serriola* L.), red-seed plantain (*Plantago rhodosperma* Decne.), clasping Venus'-looking-glass [*Triodanis perfoliata* (L.) Nieuwl.], and field pansy (*Viola bicolor* Pursh)] disappeared after the second burn and never reappeared, indicating intolerance to fire in any season.

Woody Species

Woody shrubs [e.g., rough-leaf dogwood (*Cornus drummondii* Mey.), smooth sumac (*Rhus glabra* L.), New Jersey tea (*Ceanothus herbaceous* Raf.), buckbrush (*Symphoricarpos orbiculatus* Moench), and Arkansas rose (*Rosa arkansana* Porter)] also occurred too sporadically to analyze individually. Average canopy cover of all woody species (excluding leadplant) did not change significantly through time in any burn treatment (Table 2). In ungrazed tallgrass prairie, woody species are controlled with fire (Adams et al. 1982, Hulbert 1986), and the lack of a significant change of woody cover in this study is likely due to low initial levels. Although annual fire suppresses canopy cover of woody species by removing accumulated top growth, 8 years of burning in autumn, winter, or spring did not eliminate any shrub species.

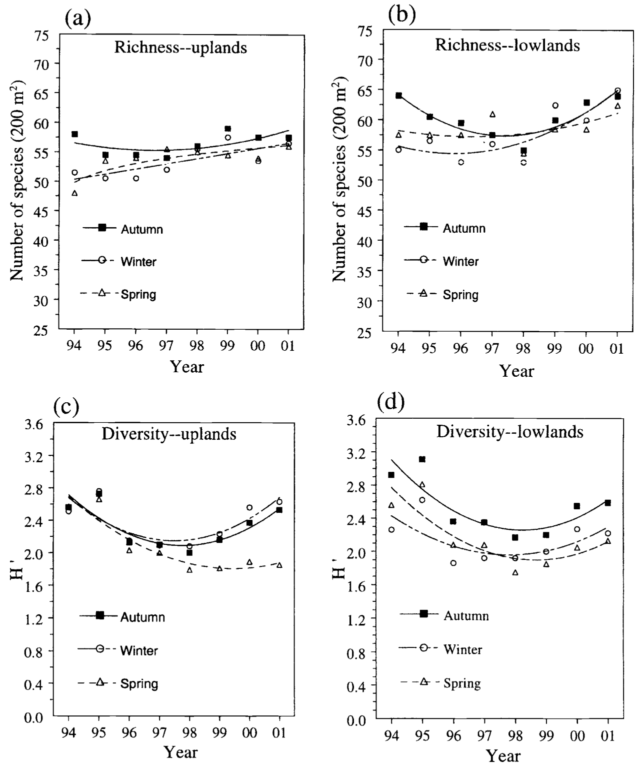

Fig 5. Changes in diversity indices through time in response to annual autumn, winter, and spring burning on different topographic positions: (a, b) species richness for upland and lowland topographic positions, (c, d) the Shannon diversity index for upland and lowland topographic positions.

Frequency of Occurrence

Depending upon topographic position, burning in any season increased the frequencies of 4 species [prairie lespedeza, round-head lespedeza (*Lespedeza capitata* Michx.), white prairie-clover (*Dalea candida* Willd.), and purple prairie-clover (*Dalea purpurea* Vent.)] (Table 3). Eight years of spring burning increased the frequency of occurrence in 15 species, compared with 10 species increasing from winter burning and 9 species increasing in response to autumn burning.

Changes in the frequency of occurrence were not always associated with concomitant changes in canopy cover. For example, the frequency of some species [white prairie-clover, purple prairie-clover, round-head lespedeza, and fringe-leaf ruellia (*Ruellia humilis*)] increased significantly in response to different burning regimes without an accompanying change in canopy cover. This suggests that burning may be important in the colonization of these species, but their density or stature is sufficiently low that changes in canopy cover are not detectable.

Diversity Indices

Species richness increased in response to spring and winter burning, but declined and then recovered to initial levels with autumn burning on both topographic positions (Fig. 5a, 5b). After 8 years of annual fire, however, the number of species on either topographic position was similar for all burn seasons. In tallgrass prairie, species richness declines as fire frequency increases (Collins et al. 1995). The trends in species richness observed in this study, however, indicated the eventual downturn requires more than 8 consecutive burns.

The effect of seasonal burning on the Shannon diversity index varied with topographic position. On upland sites, diversity declined progressively in response to annual spring burning, and declined but then recovered with both autumn and win-

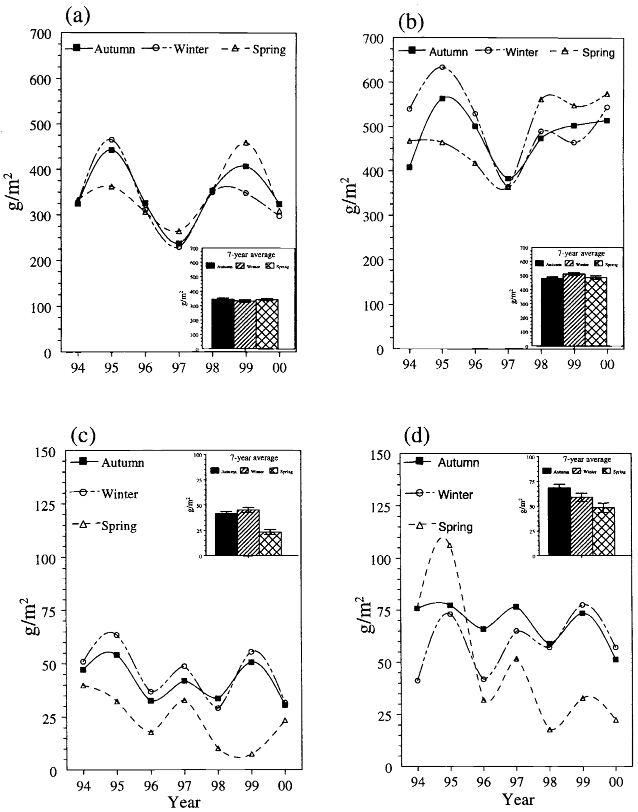

Fig. 6. Changes in biomass production in response to annual autumn, winter, and spring burning on different topographic positions: (a, b) grass biomass on upland and lowland sites, (c, d) forb biomass on upland and lowland sites. Inset in each graph represents the 7 year mean (± SE).

ter burning (Fig. 5c). On lowland sites, however, diversity decreased in response to both spring and autumn burning, and did not change through time with winter burning (Fig 5d).

Biomass

The effect of burn season on grass biomass varied inconsistently through time. Compared to spring burning, autumn fire never reduced ($P > 0.10$) grass biomass on upland sites (Fig. 6a), and winter burning reduced grass production only once (24% in 1999). In contrast, autumn and winter burning increased grass biomass 22% and 28%, respectively above spring burning on upland locations in 1995. On lowland sites, spring burning produced significantly higher grass biomass than autumn burning only in 1998, and produced more biomass than winter burning only in 1998 and 1999 (Fig. 6b). Average grass production did not differ ($P > 0.80$) among burn seasons on either uplands (Fig. 6a inset) or lowlands (Fig. 6b inset). Average forb biomass also was not different ($P > 0.30$) among burn seasons, although production was usually lowest in response to spring burning on both topographic positions (Figs. 6c and 6d). Woody biomass averaged < 2 g/m^2 on uplands and < 7 g/m^2 on lowlands, and did not differ ($P > 0.78$) among burn treatments.

Interactions among burn seasons, topographic positions, and years suggest that biomass production was likely mediated by soil moisture availability. Burning tallgrass prairie during winter or early spring is traditionally denounced because bare ground that is exposed for extended periods could potentially increase surface runoff and evaporation losses, thereby lowering soil moisture and subsequent biomass production (Hanks and Anderson 1957, Bieber and Anderson 1961, Anderson 1965, McMurphy and Anderson 1965, Owensby and Anderson 1967). Precipitation during the growing season was below normal in 5 years of this study, and if early-season burning unequivocally reduced grass biomass, it should have been apparent under these droughty conditions, particularly on the xeric uplands. Consequently, paradigms of reduced grass production from autumn or winter burning may be anomalous events from inopportune precipitation patterns, site-specific occurrences, artifacts from inadequate sampling, or confounded with livestock grazing; but they are not axiomatic for the Kansas Flint Hills.

Summary and Implications

The changes in vegetation due to repeated seasonal burning documented in this study occurred in ungrazed prairie where fire uniformly consumes the area. Response patterns may differ in grazed prairie because grazing produces a patchy burned landscape that creates numerous protective niches for species sensitive to fire. Thus, grazing can interact with seasonal burning to increase species richness and diversity (Coppedge et al. 1998). The mosaic burn patterns in grazed prairie will additionally buffer trends of many species to seasonal fire. Objectives for utilizing fire season as a management tool may vary between grazed and ungrazed prairie, but annual burning of ungrazed prairie at times other than late spring is apparently a sustainable option that does not degrade the integrity of tallgrass prairie.

Our findings contrast with many of the conventional views of how tallgrass prairie vegetation responds to seasonal fire and challenges traditional recommendations that burning should only occur in late spring. Based on these data, current decisions on managing tallgrass prairie that is burned at times other than late spring needs to be objectively reevaluated. Opposition to autumn, winter, or early spring burning is primarily an indoctrinated tenet from anti-burn campaigns in earlier decades (Hoy and Isern 1995) and inferences extrapolated from other ecosystems (Wright and Bailey 1980). In addition, fire season is often mistakenly blamed for the adverse effects from concentrated livestock grazing in pastures that have been partially burned by wildfires (Engle and Bidwell 2001). Tallgrass prairie is resilient to change, and although cover of some indigenous perennial forb species eventually increased in response to autumn and winter burning, that effect required repeated fire and did not come at the expense of warm-season grasses.

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J. Range Manage.
56: 193-197 March 2003

Prescribed fire effects on dalmation toadflax

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Abstract

Prescribed fires are important for rangeland restoration and affect plant community composition and species interactions. Many rangeland plant communities have been, or are under the threat of noxious weed invasion, however there is little information on how fire effects weeds. Our objective was to determine the effects of prescribed rangeland fire on dalmatian toadflax [*Linaria dalmatica* (L.) Miller] density, cover, biomass, and seed production. These plant characteristics, as well as density, cover, and biomass of perennial grasses and forbs were measured within burned and adjacent not-burned areas on 3 A*rtemisia tridentata/Agropyron spicatum* habitat types in Montana. Areas were burned in the spring and measured in the fall 1999. Comparisons of plant characteristics between the burned and not-burned sites were made using t-tests and non-parametric Wilcoxon Rank Sum tests. After 1 growing season, fire did not affect density or cover of dalmatian toadflax. Burning increased dalmatian toadflax biomass per square meter at 2 sites, and per plant biomass at all 3 sites. Seed production of dalmatian toadflax was increased by fire at all 3 sites. Fire reduced forb cover at 1 site and increased grass biomass at 2 sites. The increases in dalmatian toadflax biomass and seed production suggest that fire used to restore healthy plant communities may increase dalmatian toadflax dominance. We recommend weed management procedures, such as herbicide control and seeding desirable species, be integrated with prescribed fire where dalmatian toadflax is present in the plant community.

Key words: *Linarea dalmatica*, noxious rangelands weeds, integrated weed management.

Resumen

Los fuegos prescritos son importantes para la restauración de los pastizales y afectan a la composición de las comunidades de plantas y la interacción entre especies. Muchas comunidades vegetales de pastizal han sido invadidas o están bajo la amenaza de ser invadidas por malezas nocivas, sin embargo, hay poca información sobre como el fuego afecta las malezas. Nuestro objetivo fue determinar los efectos del fuego prescrito en el pastizal sobre la densidad, cobertura, biomasa y producción de semilla de "Dalmatian toadflax" [*Linaria dalmatica* (L.) Miller]. Estas características de la planta, asi como la densidad, cobertura y biomasa de zacates perennes y hierbas, se midieron dentro de áreas quemadas adyacentes a áreas no quemadas en 3 hábitats del tipo *Artemisia tridentata/Agropyron spicatum* de Montana. Las áreas fueron quemadas en primavera y medidas en otoño de 1999. Las comparaciones de las características de las plantas entre los sitios quemados y no quemados se realizaron mediante pruebas de t y la prueba no paramétricas de la Suma del Rango de Wilcoxon. Después de una estación de crecimiento, el fuego no afecto la densidad o cobertura del "Dalmatian toadflax". La quema incrementó la biomasa por metro cuadrado de "Dalmatian toadflax" en 2 sitios y la biomasa por planta en los 3 sitios. La producción de semilla de "Dalmatian toadflax" se incremento con el fuego en todos los sitios. El fuego redujo la cobertura de hierbas en un sitio e incremento la biomasa de zacates en 2 sitios. El incremento de biomasa y producción de semilla de "Dalmatian toadflax" sugieren que el fuego utilizado para restaurar comunidades vegetales saludables puede incrementar la dominancia de "Dalmatian toadflax". Nosotros recomendamos que donde el "Dalmatian toadflax" este presente en la comunidad vegetal se integren procedimientos de manejo de maleza, tales como control con herbicidas y siembras de especies deseables, con el fuego

Dalmatian toadflax [*Linaria dalmatica* (L.) Miller] is a rhizomatous, perennial weed native to the Mediterranean region. It was brought to the west coast of North America as an ornamental about 1874 and has spread throughout the western states, British Columbia and Alberta (Alex 1962). Because of high genetic variability, dalmatian toadflax is adapted to a wide variety of habitat conditions but favors well-drained, relatively coarse-textured soils (Lajeunesse 1999). Dalmatian toadflax is an aggressive competitor because of early spring regeneration from vegetative buds on root stocks and rhizomes buried in the soil, and because of its high seed production. Infestations of dalmatian toadflax may reduce desirable plants causing loss of winter forage for wildlife (Lajeunesse 1999), reduce cattle-carrying capacity, and reduced appraised ranchland value (Lacey and Olsen 1991). Cattle occasionally browse flowering shoots, but usually avoid this weed (Harris and Carter 1971).

Fire is a natural disturbance of ecosystems that can change community structure and function, at least in the short-term (Ueckert et al. 1978, Sharrow and Wright 1977, Whittaker 1961). Prescribed burning has been used to increase diversity, reduce shrub and tree encroachment, and control excess litter buildup on rangeland for centuries. In most cases, the target species for management with fire have been indigenous, including junipers (Juniperus) and pines (Pinaceae). During the last 50 years, many

Funding for this study was provided by the USDI Bureau of Land Management and the Rocky Mountain Elk Foundation. Study sites were contributed by the USDI Bureau of Land Management and USDA Forest Service. Personnel and resources for conducting the burns were contributed by the USDI Bureau of Land Management and USDA Forest Service.
Manuscript accepted 29 May 2002.

North American rangelands have been invaded by, or are under the threat of invasion by non-indigenous species. There are few studies, however, that quantify the effects of fire on noxious rangeland weeds, and no studies on fire effects on dalmatian toadflax.

Alterations in community structure and function caused by rangeland fire may affect invasibility of an ecosystem or the ability of an existing invader to reach dominant status. On *Artemisia* steppe communities, establishment of cheatgrass (*Bromus tectorum* L.) communities can be enhanced by fire. Increased build-up of the continuity of fine fuels from cheatgrass causes self perpetuating, larger, and more frequent fires that favors cheatgrass reproduction and suppresses native perennial grasses (Pellant 1990, Peters and Bunting 1994). A single low intensity fire increased the cover and density of diffuse (*Centaurea diffusa* Lam.) and spotted knapweeds (*C. maculosa* Lam.) in northern Washington (Sheley and Roché 1982). In Montana, there is evidence that spotted knapweed increased sixfold within 2 years after a controlled fire on a forested site (Rice and Sacco 1995). Nutrients released from plant litter, and the disturbance created by fire may favor growth and reproduction of weedy species with early germination and rapid growth characteristics (Sheley et al. 1998). The objectives of this study were to determine the short-term effects of a single spring prescribed fire on the cover, density, biomass, and seed production of dalmatian toadflax. We hypothesized that dalmatian toadflax cover, density, biomass and seed production would increase after burning.

Methods

Study Sites

The study was conducted within an *Artemisia tridentata/Agropyron spicatum* (Mueggler and Stewart 1980) habitat type on 3 sites located in the foothills of the Elkhorn Mountains, southeast of Boulder, Mont. The area was managed for elk (*Cervus elaphus*) range and had not been grazed by livestock for 10 years. Prescribed burns in the area were designed to improve wildlife habitat by creating a diverse mosaic of open parks, and the prescription to burn was based on the presence of woody species. Targeted encroachment tree and shrub species including limber pine (*Pinus flexilis* James), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), big sagebrush (*Artemisia tridentata* Nutt.) and rubber rabbitbrush (*Chrysothamnus nauseosus* (Pallas ex Pursh) Britt). Monthly summaries for precipitation in the area encompassing all 3 sites are summarized for the year before the burn (1998), the year of the burn (1999), and the 30 year (1961–1990) average (Table 1).

Table 1. Monthly summary from 1998, 1999, and the 30-year average of precipitation (mm) for Elk Horn, Mont., the area of the 3 sites.

	1998	1999	30 Yr Average
	(mm)		
January	6	4	15
February	2	4	9
March	3	1	15
April	12	14	21
May	34	39	47
June	87	65	50
July	32	9	35
August	13	63	35
September	29	6	30
October	9	1	14
November	16	6	13
December	12	4	13
Annual	256	214	297

Site 1 was located in Wood Gulch (46° 13.002' N, 111° 5.094' W) at an elevation of 1,750 m. Slope ranged from 15 to 35% with a southern aspect. Soils were Maiden-Lap-rock outcrop complex consisting of loamy-skeletal, carbonatic Typic Calciborolls. The predominant grasses at Wood Gulch were bluebunch wheatgrass (*Agropyron spicatum* (Prush) Scribn. & Smith) and Idaho fescue (*Festuca idahoensis* Elmer). Site 2 was in Upper Horse Gulch (46° 12.140' N, 111° 55.408' W) at an elevation of 1,825 m. Slope ranged from 15 to 45% with an eastern aspect. Upper Horse Gulch soils were Whitcow, Bouldery-Shawmut, very bouldery-rock outcrop complex consisting of loamy-skeletal, mixed Typic Argiborolls and loamy-skeletal, carbonatic, frigid Calcic Ustochrepts. Grasses were predominantly bluebunch wheatgrass and prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schultes). Site 3 was in Lower Horse Gulch (46° 13.348' N, 111° 55.111' W) at an elevation of 1,635 m. Slope averaged 15% and the aspect was southeast. Soils were Windham-Lap very cobbly loams consisting of loamy-skeletal, carbonatic Typic Calciborolls. Grasses were bluebunch wheatgrass, prairie Junegrass, blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Griffiths), and red threeawn (*Aristida prupurea* Nutt). Plant species present at the time of sampling for the 3 sites are listed in Table 2.

Table 2. Plant species present (% of 40 plots) at Wood Gulch, Upper Horse Gulch and Lower Horse Gulch sites at the time of sampling.

Plant species	Wood	Upper Horse	Lower Horse
		(% of 40 plots)	
Achillea millefolium (L.)	5	23	15
Agropyron spicatum (Pursh) Gould	97	100	95
Antennaria parvifolia (Nutt.)	13	28	15
Arnica diversifolia (Greene)	0	8	0
Aristida purpurea (Nutt.)	3	0	8
Artemesia tridentata (Nutt.)	5	20	3
Astragalus spp.	0	5	5
Bouteloua gracilis (H.B.K.) Lag.	0	0	5
Chrysothamnus viscidiflorus (Hook)	13	0	25
Cirsium undulatum (Nutt.)	0	3	3
Erigeron ochroleucus (Nutt.)	20	20	5
Festuca idahoensis (Elmer)	35	93	60
Juniperus scopulorum (Sarg.)	0	0	3
Linaria dalmatica (L.)	40	100	60
Linum lewisii (Pursh)	15	18	5
Opuntia polyacantha (Haw.)	0	0	8
Oryzopsis hymenoides (Roem. and Schult.)	25	10	10
Phlox hoodii (Richardson)	10	40	15
Poa secunda (Presl)	80	72	83
Stipa comata (Trin. and Rupr.)	5	15	5
Taraxacum officinale (Weber)	5	8	13
Thermopsis montana (Nutt.)	0	3	0
Tragopogon dubius (Scop.)	10	43	13

Experimental Design and Sampling

The experimental design was a comparison of 2 treatments, burned and not-

Table 3. Prescribed burn conditions at the 3 sites.

Site	Size	Date of burn	Wind	Air temp.	RH	Flame length	Rate of spread
	(ha)		(km hr^{-1})	(°C)	(%)	(m)	(m^2 hr^{-1})
Wood Gulch	80	11/3/99	0-10	14	30-80	1.0	200
Upper Horse Gulch	60	16/3/99	0-10	16	30-50	1.5	250
Lower Horse Gulch	40	16/3/99	0-10	18	30-40	1.5	250

burned. The burn treatments for the 3 sites are described in Table 3. Comparisons were made by sampling 20 randomly selected 0.44 m^2 circular plots within the burns and 20 independent randomly selected plots within immediately adjacent non-burned areas at each of the 3 sites. Soil and species composition in the burned and non-burned areas were identical at each site. Sites were sampled from 29 September through 8 October 1999. The experiment was not replicated in time because of the aggressive herbicide control of the dalmatian toadflax, and therefore it was replicated in space by using 3 sites. All species were counted within sample plots and the area of ground covered by species was visually estimated as a percent of the total area. Each dalmatian toadflax rosette or flowering stem was counted as an individual. Each bunchgrass was counted as an individual. All plants within the circle were then clipped to ground level by species, oven dried (60°C) to constant weight and weighed. Seed pods of dalmatian toadflax were separated from other vegetative material and seeds were extracted and counted.

Data Analysis

Sites differed in dalmatian toadflax density and were analyzed separately. Differences between burned and non-burned treatments in density, cover, biomass per square meter, per plant biomass, per plant seed production of dalmatian toadflax, and density, cover and biomass of perennial grass and perennial forbs other than dalmatian toadflax were determined using a 2 sample t-test procedure (SAS Institute Inc. 1990). An F' (folded) statistic was calculated to test for equality of the 2 variances. When normality or equality of variances were not reasonable (Prob. $F \leq 0.05$), data were analyzed using the non-parametric Wilcoxon Rank Sum test (SAS Institute Inc. 1990).

Results

Precipitation

The 30 year average annual precipitation for the area was 297 mm (Table 1). Annual precipitation in 1998, the year before the prescribed burns was 14 % below the 30-year average and 28% lower in 1999, the year of the burns. Precipitation during June and August of 1999 were 29 and 79% above the 30-year average, for those months, respectively

Density

Burning did not affect dalmatian toadflax density the season following burning at any of the 3 sites ($P > 0.05$, Table 4). Rosette and mature stem density responses were similar to total density and therefore only total density is presented. At Wood Gulch, dalmatian toadflax was present in 40% of the plots sampled with mean density of 20 plants m^{-2} in the burned plots and 43 plants m^{-2} in the not-burned plots. Dalmatian toadflax was present in 100% of the plots at Upper Horse Gulch and its density was 141 and 154 plants m^{-2} in the burned and not-burned plots, respectively. At Lower Horse Gulch, dalmatian toadflax was present in 60% of the plots sampled with mean density of 30 plants m^{-2} in the burned plots and 25 plants m^{-2} in the not-burned plots. There was no difference between the burn treatments in the density of perennial grass or perennial forbs (Table 4).

Cover

Burning did not affect dalmatian toadflax cover the season following burning at any of the 3 sites ($P > 0.05$, Table 4). At Wood Gulch, dalmatian toadflax cover averaged 2.8% in the burned plots and 2.2% in the not-burned plots. Dalmatian

Table 4. Means of density (m^{-2}), cover (%), biomass (m^{-2} and per plant for toadflax), and toadflax seed production (per plant) for dalmatian toadflax, perennial grass, and perennial forbs at Wood Gulch, Upper Horse Gulch and Lower Horse Gulch for the burn and not-burn treatments. Differences between burn and not-burn treatments are indicated by an asterisk before the means.

Site	Variable	Toadflax burn	No burn	Grass burn	No burn	Forbs burn	No burn
Wood	Density 20 (plants m^{-2})		43.0	180.0	202.0	22.0	23.0
Wood	Cover (%)	2.8	2.2	25.4	23.9	1.9	2.8
Wood	Biomass (g m^{-2})	17.0	8.0	*70.5	*40.0	2.4	4.9
Wood	Per plant biomass (g $plant^{-1}$)	*4.2	*1.0				
Wood	Seed production (no. $plant^{-1}$)	*355.0	*7.0				
Upper Horse	Density	141.0	154.0	142.0	130.0	63.0	60.0
Upper Horse	Cover	7.8	6.2	23.1	25.3	5.9	2.9
Upper Horse	Biomass	*53.0	*31.0	28.9	48.4	8.6	16.2
Upper Horse	Per plant biomass	*7.1	*1.1				
Upper Horse	Seed production	*158.0	*79.0				
Lower Horse	Density	30.0	25.0	177.0	172	36.5	18.5
Lower Horse	Cover	5.7	2.7	24.9	21.9	7.6	4.4
Lower Horse	Biomass	*38.0	*8.0	*73.0	*45.0	20.7	16.3
Lower Horse	Per plant biomass	*7.3	*2.0				
Lower Horse	Seed production	*1,328.0	*29.0				

toadflax cover at Upper Horse Gulch was 6.2 and 7.8% in the not-burned and burned plots, respectively. Cover at Lower Horse Gulch averaged 2.7 and 5.7% in the not-burned and burned plots, respectively. Burning did not affect perennial grass cover at any site. Perennial forb cover was reduced by burning from 5.9% in the plots that were not burned to 2.8 in the burned plots at Upper Horse Gulch (Table 4).

Biomass

The influence of fire on dalmatian toadflax biomass per square meter varied depending on site (Table 4). At Wood Gulch where dalmatian toadflax was absent from 60% of the plots, the fire effect was not significant even though the biomass was twice as high on plots that burned (17 g m^{-2}) compared to those that did not (8 g m^{-2}). On Upper Horse Gulch where dalmatian toadflax occurred on all plots, fire increased dalmatian toadflax biomass from 31 g m^{-2} where there was no fire to 53 g m^{-2} where there was fire. Fire increased dalmatian toadflax biomass from 8 to 38 g m^{-2} on the not-burned plots compared to burned plots at Lower Horse Gulch where dalmatian toadflax occurred on 60% of the plots.

Fire increased dalmatian toadflax per plant biomass at all sites (Table 4). At Wood Gulch, dalmatian toadflax biomass was 1.0 g per plant in the plots that were not burned and 4.2 g per plant in the burned plots. Dalmatian toadflax increased from 1.1 to 1.7 g per plant in the not-burned and burned plots, respectively, at Upper Horse Gulch. Dalmatian toadflax biomass in the not-burned plots at Lower Horse Gulch was 2.0 g per plant compared to 7.3 g per plant in the burned plots.

Fire increased perennial grass biomass at Wood and Lower Horse Gulches, but there was no difference at Upper Horse Gulch. Perennial grass biomass production at Wood Gulch was 40.8 g m^{-2} where there was no burning and 70.5 g m^{-2} where it was burned. Upper Horse Gulch perennial grass biomass was 28.9 and 48.4 g m^{-2} in the burned compared to not-burned plots, respectively. At Lower Horse Gulch, perennial grass biomass increased from 45.1 to 73.0 g m^{-2} in the not-burned compared to the burned treatments. Fire did not affect perennial forb biomass (Table 4).

Dalmatian Toadflax Seed Production

Burning dramatically increased dalmatian toadflax seed production per plant at all 3 sites (Table 4). Burning increased seed production from 7 to 355 seeds per plant at Wood Gulch, from 79 to 158 seeds per plant at Upper Horse Gulch, and from 29 to 1,328 seeds per plant at Lower Horse Gulch.

Discussion

It is not surprising that there was no short-term burning effect on dalmatian toadflax, perennial grass, or perennial forb density. The heat intensities of the burns at the 3 sites were considered normal for spring fires by technicians conducting the burns (USDA Forest service, personal communication). Many bunchgrass clumps and dalmatian toadflax rosettes were still green after burning and dalmatian toadflax rhizomes were generally below 10 mm of soil and not damaged by fire generated heat (Hayward 1938). It is doubtful that the thermal death point for plant tissue was reached during the fires (Write 1970, Wright et al. 1976).

Maximum temperatures in shrubland fires are always near the top of the vegetation (Bailey and Anderson 1980, Whittaker 1961), killing shrub and tree species with perennating buds in this zone. The removal of big sagebrush and pine species by the prescribed burns in this study opened niches once occupied by these species and made available resources they used. The reduced competition for resources could partly explain the increase in biomass of dalmatian toadflax and perennial grass, and the increased seed production of dalmatian toadflax in the burned areas. We expect future increases of dalmatian toadflax because large areas once occupied by trees and shrubs were left open to invasion by high seed producing dalmatian toadflax especially on the Upper Horse Gulch site where there were fewer perennial grasses to fill open niches.

On semi-arid rangelands, nutrients bound in living and dead biomass are made available for plant growth by fire (DeBano and Conrad 1978). In addition, soil conditions after burning often favor nitrification (Sharrow and Wright 1977). Increases in dalmatian toadflax and grass biomass in the burned areas may have occurred because of increased nutrients. On a different burn under similar conditions, nitrate increased ($P = 0.002$) from 3.3 mg kg^{-1} on plots that did not burn to 7.6 mg kg^{-1} on plots that burned (Jacobs unpublished data). This offers another explanation to the increase in dalmatian toadflax and grass biomass in the burned areas. The lack of grass response at Upper Horse Gulch suggests that there was less grass present to respond to increased nutrients, or dalmatian toadflax was dense enough to overwhelm the grass. Nitrate is mobile and rapidly used by plants and therefore high nitrate conditions may favor weeds with early and rapid growth characteristics (Sheley et al. 1998) over native grasses that tend to have less aggressive growth characteristics.

The more robust dalmatian toadflax plants produced 2- to 10-fold more seeds in the burned areas compared to areas not-burned. While we did not detect increases in dalmatian toadflax density in the season following fire, increased seed production suggests that we can expect increases in toadflax density and spread on these sites in the future. Increases in the density of other invasive non-indigenous species have been reported. Sheley and Roché (1982) found increased cover and density of diffuse and spotted knapweeds in northern Washington, and Rice and Sacco (1995) report a sixfold spotted knapweed increase in Montana within 2 years after a controlled fire on a forested site.

Conclusions

Our results suggest fire will not reduce dalmatian toadflax populations on rangeland and may increase the dominance of this weed. We recommend implementing an integrated dalmatian toadflax management program when conducting a prescribed burn for restoring native plant communities and controlling encroaching undesirable plants. Integrated practices could include herbicide application to reduce dalmatian toadflax density and seed production, and seeding with desirable plant species to fill niches opened by fire.

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56: 198-202 March 2003

Overcoming dormancy in New Mexico mountain mahogany seed collections

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Abstract

Mountain mahogany (*Cercocarpus montanus* Raf) is a useful reclamation species because it can occupy and improve poor soils. Literature regarding seed propagation of this species is varied and often contradictory, recommending stratification durations of 14 to 90 days, and sulfuric acid scarification durations of none to 60 minutes. To assess variability in propagation requirements among seed sources, 8 New Mexico seed sources were tested with factorial combinations of scarification and stratification treatments. Sources were selected to encompass both a range of latitudes throughout New Mexico and a range of elevations at Questa, N. M. Seeds were scarified 5 or 10 minutes in concentrated sulfuric acid, tumbled 5 or 10 days in course grit, or unscarified (control). Seeds underwent subsequent stratification for 0 (control), 30, or 60 days. Averaged across scarification treatments, the 2 southernmost sources lacked a stratification requirement, while northern seed sources achieved their highest germination following the longest stratification duration (60 days). Improvement in germination due to stratification was greatest for the 2 highest elevation Questa sources. Scarification treatments were less effective in improving germination than stratification treatments, and produced more variable results. A 5-minute soak in sulfuric acid was the most effective scarification treatment, but for 2 sources, this treatment reduced germination. Variability in the stratification requirement appears to be an adaptation to macroclimatic differences among seed sources, whereas differential response to scarification may be a response to microclimatic differences.

Key Words: acid scarification, stratification, ecotypic variability, *Cercocarpus montanus*

Resumen

El "Mountain mahogany" (*Cercocarpus montanus* Rat) es una especie útil para la restauración de pastizales porque puede ocupar y mejorar suelos pobres. La literatura respecto a la propagación de semilla de esta especie es variada y a menudo es contradictoria, recomendando periodos de estratificación de 14 a 90 días y tiempos de escarificación con ácido sulfúrico de nada a 60 minutos. Para evaluar la variabilidad en requerimientos de propagación entre fuentes de semilla se evaluaron 8 fuentes de semilla provenientes de New Mexico en combinación factorial de tratamientos de escarificación y estratificación. Las fuentes de semilla fueron seleccionadas para abarcar un rango de altitudes a través de New Mexico y un rango de elevaciones en Questa, N. M. Las semillas fueron escarificadas por 5 o 10 minutos en ácido sulfúrico concentrado, agitadas 5 o 10 días en una cama de arena o sin escarificar (control). Las semillas recibieron una estratificación subsecuente de 0 (control), 30 o 60 días. Promediando a través de los tratamientos de escarificación, se detectó que las dos fuentes de semilla de mas al sur no requirieron de estratificación, mientras que las fuentes de semilla del norte alcanzaron los más altos porcentajes de germinación con el tratamiento de estratificación mas largo (60 días). La mejoría en la germinación debida a la estratificación fue mayor para las 2 fuentes de semilla de mayor altitud en Questa. Los tratamientos de escarificación fueron menos efectivos en mejorar la germinación que los tratamientos de estratificación y produjeron resultados más variables. Un remojo de 5 minutos en ácido sulfúrico fue el tratamiento de escarificación más efectivo, pero para en dos fuentes de semilla este tratamiento redujo la germinación. La variabilidad en los requerimientos de estratificación parece ser una adaptación las diferencias macroclimáticas entre las fuentes de semilla, mientras que la respuesta diferencial a la escarificación puede ser una respuesta a diferencias microclimáticas.

Mountain mahogany (*Cercocarpus montanus* Raf) occupies sites that are dry, unstable, erosive, and of low fertility (Brotherson 1992), and is actinorhizal, forming a nitrogen-fixing symbiosis with *Frankia* bacteria (Paschke 1997). These characteristics make it an excellent shrub species for reclamation in the western United States. Poor germinability has proven to be an obstacle to production of seedlings for revegetation, and propagation literature is inconsistent and often contradictory.

Published literature recommends stratification at 0 to 5°C, but recommended treatment durations vary from 14 to 90 days (Hervey 1955, Heit 1970, Smith 1971, Deitschman et al. 1974, Kitchen and Meyer 1990). Kitchen and Meyer (1990), studying Utah and Colorado seed sources, found the stratification requirement to vary from 42 to 84 days depending on source. Although the seed coat of mountain mahogany is permeable to water (Heit 1970), scarification treatments have been effective in promoting germination. Hervey (1955) reported that a 60-minute soak in acid improved germination. Dreesen (unpublished data) found incubation in acid for as short as 5 minutes to result in complete

This research was funded, in part, through grants from McIntire Stennis, Molycorp Inc. of Questa, N.M., and the New Mexico Agriculture Experiment Station.

Manuscript accepted 12 Jun. 02

Table 1. Sources of mountain mahogany seed collected in September and October 1997 and used in germination studies.

Source	Latitude	Location	Elevation
Capulin	36°42'N	Molycorp Mind-Questa, N.M.	2,987 m
Blind Gulch	36°42'N	Molycorp Mind-Questa, N.M.	2,896 m
Mahogany Hill	36°42'N	Molycorp Mind-Questa, N.M.	2,774 m
Headframe Hill	36°42'N	Molycorp Mind-Questa, N.M.	2,560 m
Boxcar	36°42'N	Molycorp Mind-Questa, N.M.	2,499 m
Rociada	35°50'N	Rociada, N.M.	2,377 m
Sandia	35°10'N	Cibola National Forest, N.M.	2,835 m
Sacramento	32°58'N	Lincoln National Forest, N.M.	2,621 m

seed destruction. Heit (1970) found that a 10-minute soak in acid increased germination speed but not percentage, while a 20-minute soak injured seeds.

Inconsistencies among propagation protocols for mountain mahogany may be related, in part, to extensive ecotypic variability (Young et al. 1978). This study was undertaken to assess variability in response to stratification and scarification treatments among 8 New Mexico collections of mountain mahogany selected across latitudinal and elevational gradients.

Materials and Methods

Seeds were collected from 8 New Mexico sources (Table 1). Sources were selected to encompass both a range of latitudes throughout New Mexico and a range of elevations at Molycorp Mine in Questa, N.M. Seeds were collected from a minimum of 5 plants at each source. Seeds were considered ripe when easily removed from the plant. Styles were separated from seeds in a rubbing box, and seeds were then separated from debris in a Dakota blower. Cleaned seeds were stored at 5°C for over 2 years until the start of the study. At this temperature, seeds retain viability for at least 6 years (Springfield 1973).

Limited seed availability restricted the number of sulfuric acid and dry-tumble scarification treatments imposed on 3 of 8 sources used in this study. As a result, the study consisted of 2 overlapping experiments generating 2 data sets. The first experiment tested a factorial combination of all 8 seed sources, 3 scarification treatments (unscarified control, 5-minute sulfuric acid soak, and 5-day dry-tumble treatment), and 3 stratification lengths (0, 30, or 60 days). The second experiment evaluated a factorial combination of 5 seed sources, 5 scarification treatments (unscarified control, 5-minute sulfuric acid soak, 10-minute sulfuric acid soak, 5-day dry-tumble treatment, and 10-day dry tumble treatment) and 3 stratification lengths (0, 30, or 60 days). Results for the second experiment are presented only in regards to the 2 additional scarification treatments. Each treatment combination was tested with four, 100-seed replications. Due to missing data, the Sacramento source was not included in statistical comparisons. However, some germination data are presented for reference.

Seeds undergoing acid scarification were soaked in concentrated sulfuric acid (Reagent ACS, 95.0 to 98.0%, VWR), then thoroughly rinsed under running tap water. Seeds underwent dry-tumble scarification mixed with 10 g course grit (True Square Metal Products) in a 4-ounce round ointment tin (US Can), which was placed within the canister drum of a No. 140 Model B High Speed Tumbler (Trusquare Metal Products) turning at approximately 40 rpm. Tins were tightly packed in the canister drum, so that each can rotated 360 degrees for each 360-degree rotation of the drum.

Before undergoing stratification treatment (or germination testing for stratification-control seeds) all seeds were soaked for 1 minute in hydrogen peroxide (VWR 3% Stabilized) for surface sterilization and thoroughly rinsed under running tap water. This step was undertaken to minimize potential differences in seed contamination between acid-treated and non-acid-treated seeds, which could have biased the results. Hydrogen peroxide can affect germination. However, when used as a seed pretreatment, much longer soak durations and/or higher concentrations are typically used (Young and Evans 1981, Rosner 2000).

Seeds undergoing stratification were spread evenly over half of a 20 x 20 cm piece of cotton cloth that had been saturated with distilled water. The cloth was folded to enclose the seeds, placed within 15 x 16 cm self-sealing poly bags, and covered with 200 ml peat moss, which had been saturated with distilled water and squeezed by hand to remove excess water. Poly bags were placed in a walk-in cooler maintained near 5°C for the duration of stratification treatment.

Seeds were tested for germination between two, 20.5 cm filter papers (VWR Grade 413 Qualitative) saturated with distilled water. Filter papers were sealed in 1-gallon self-sealing poly bags, which were placed on greenhouse benches. Thermostat settings in the greenhouse were adjusted to maintain daytime highs near 30°C and nighttime lows near 15°C. Although testing germination over a wide range of controlled temperature regimes is necessary to fully characterize dormancy, germination testing was conducted in this manner to characterize the expression of dormancy in a typical greenhouse setting. Optimal germination temperature for this species varies among seed sources (Piatt 1976, Smith 1971, Smith and Bass 1973,

Table 2. Categorical analysis of variance tables for effect of scarification, stratification, seed source, and interactions of these factors on mountain mahogany germination.

8-Source Experiment[1]	Component	df	Chi-Square	Observed Significance	5-Source Experiment	Component	df	Chi-Square	Observed Significance
-Control, 5-minute acid soak, and 5-day dry-tumble scarification treatments.	Scar[2]	2	13.3	<.001	*-All scarification treatments (5).*	Scar[2]	4	90.9	<.0001
	Strat	2	393.0	<.0001		Strat	2	326.8	<.0001
	Source	6	3710.5	<.0001	*-Blind Gulch, Mahogany Hill, Headframe Hill, Boxcar, and Sandia seed sources.*	Source	4	4197.9	<.0001
-Capulin, Blind Gulch, Mahogany Hill, Headframe Hill, Boxcar, Rociada, and Sandia seed sources.	Scar by Strat	4	105.3	<.0001		Scar by Strat	8	147.6	<.0001
	Scar by Source	12	276.9	<.0001		Scar by Source	16	384.6	<.0001
	Strat by Source	12	159.3	<.0001		Strat by Source	8	120.5	<.0001
	Scar by Strat by Source	24	121.3	<.0001		Scar by Strat by Source	32	209.2	<.0001

[1]Sacramento source was dropped from this analysis leaving 7 sources.
[2]Scar=Scarification. Strat=Stratification

Table 3. Mean germination percentages and standard errors for data averaged across stratification and scarification (control, 5-minute acid soak, 5-day dry-tumble) treatments for each mountain mahogany seed source.

Seed Source	Mean Germination	Standard Error
	(%)	
Capulin	19.6	0.7
Blind Gulch	21.6	0.7
Mahogany Hill	44.6	0.8
Headframe Hill	82.1	0.6
Boxcar	64.8	0.8
Rociada	61.9	0.8
Sandia	53.8	0.8
Sacramento	28.8	0.8

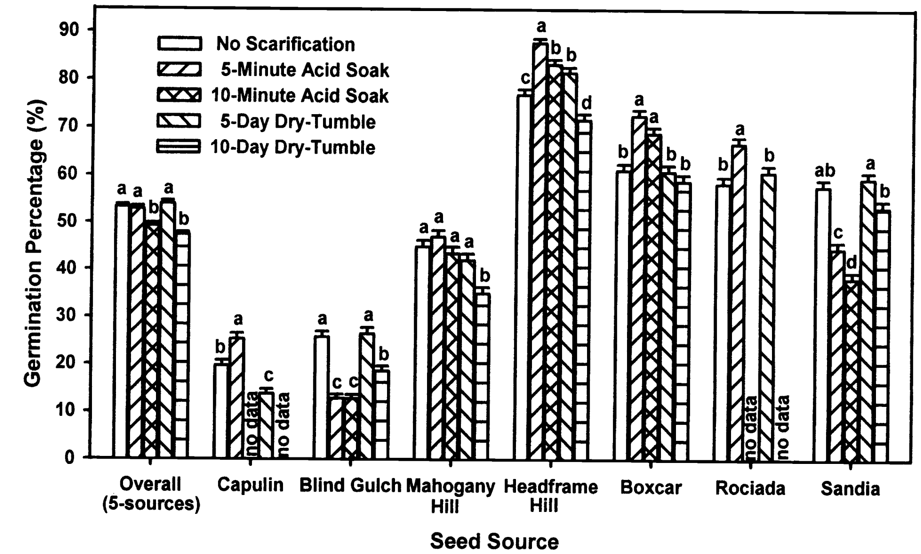

Fig. 2. Effect of scarification treatment and its interaction with seed source (averaged across stratification treatments) on mountain mahogany germination. Means labeled with the same letter are not significantly different at $\alpha = (0.05)/3$—where 3 treatments are compared and $\alpha = (0.05)/10$—where 5 treatments are compared.

Kitchen et al. 1989). Greenhouse temperatures during the germination test ranged from 28.2°C * 0.5°C for mean daytime highs to 13.9°C * 0.3°C for mean nighttime lows. Paper moisture level was maintained by application of distilled water as needed. Seeds were checked for germination after 0, 7, 14, 21, and 28 days. Seeds were considered germinated when the radical had emerged through the seed coat.

Categorical analysis of variance (SAS Proc CATMOD, SAS Institute 1989) was used to determine treatment differences in germination using a factorial treatment structure. Analysis was also run separately by seed source. (Traditionally, analysis of variance [ANOVA] has been used to analyze germination data. The ANOVA assumes continuous, normally distributed data with equal variances, but germination percentage data has unequal variances between treatments and is frequently skewed and, therefore, non-normal. Usually percentage data are arcsine transformed to achieve normality and then analyzed by ANOVA. Until, the advent of high-speed microcomputers, use of more appropriate categorical models for analysis of germination data was impractical.) Categorical analysis of variance is a generalization of the chi-square (X^2) test of homogeneity. The maximum-likelihood technique was used to calculate X^2 test statistics. Observed significance levels less than 0.05 were considered significant. Percentages and standard errors were calculated for main effects and interaction combinations. Approximate pairwise Z-statistics were used to conduct pairwise comparisons of main treatment effects using a conservative alpha value of 0.05 divided by the number of comparisons.

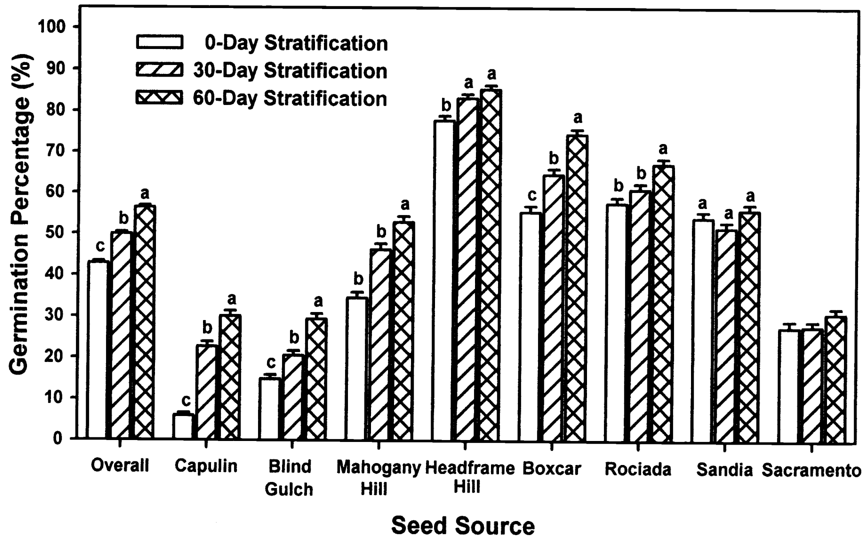

Fig. 1. Effect of stratification and its interaction with seed source (averaged across 3 scarification treatments) on mountain mahogany germination. Pairwise comparisons were omitted for the Sacramento source because they would be biased by a missing treatment combination. Germination means labeled with the same letter are not significantly different at $\alpha = (0.05)/3$.

Results

In both the 8-source and the 5-source experiments, scarification, stratification, seed source, and all interactions of factors affected germination (Table 2). Seed source had the greatest effect on germination. Germination percentages were highly variable among sources (Table 3) and were improved by stratification (for data averaged over seed sources and scarification treatments). A 60-day treatment was most effective (Fig. 1). Differences in response to stratification among seed sources (for data averaged across scarification treatments) conformed to a latitudinal gradient with germination improving in response to increasing stratification duration only for the 6 northern sources (all except Sandia and Sacramento) (Fig. 1). Percentage improvement due to stratification was greatest for the 2 Questa seed sources from highest elevation (Capulin and Blind Gulch) and least for the 3 southernmost sources (Rociada, Sandia, and

Table 4. Improvement in mountain mahogany germination (percentage and SE) by seed source due to stratification treatment, for data averaged across 3 scarification treatments (control, 5-minute acid soak, 5-day dry-tumble).

Stratification Duration	Capulin	Blind Gulch	Mahogany Hill	Headframe Hill	Boxcar	Rociada	Sandia	Sacramento
	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
0	5.9 (0.7)	14.8 (1.0)	34.6 (1.4)	77.8 (1.2)	55.4 (1.4)	57.6 (1.4)	54.0 (1.4)	27.5 (1.6)
30 days	22.7 (1.2)	20.6 (1.7)	46.3 (1.4)	83.2 (1.1)	64.5 (1.4)	60.9 (1.4)	51.5 (1.4)	27.7 (1.3)
60 days	310.1 (1.3)	29.4 (1.3)	52.9 (1.4)	85.3 (1.0)	74.4 (1.3)	67.1 (1.4)	55.8 (1.4)	30.8 (1.3)
Improvement following 60-day stratification relative to control	410%	99%	53%	10%	34%	16%	3%[1]	12%[2]

[1]Germination percentages were not significantly different.
[2]Significance of improvement not tested because of missing treatment combinations.

Sacramento) and one northern source (Headframe Hill) (Table 4).

Scarification also affected germination percentage. Although no scarification treatment improved germination relative to control seeds for data averaged over seed sources, some treatments were effective for individual sources (Fig. 2). Acid scarification improved germination for 4 of 7 seed sources tested, but reduced germination for 2 seed sources. Dry-tumble scarification (averaged across stratification treatments) had little influence on germination, increasing germination for only 1 seed source. For the 5 sources evaluated, as scarification duration increased from either a 5-minute to a 10-minute acid soak or from a 5-day to a 10-day tumble scarification, total germination was either unaffected or reduced.

Response to scarification varied across stratification treatments (Fig. 3). Averaged across seed sources, the best acid soak (5 minutes) and dry-tumble (5-day) treatments improved germination appreciably only when no stratification was used. The interaction between stratification and scarification also varied among seed sources (Fig. 4). For 5 of 8 seed sources, benefit of scarification was lost when stratification was increased to 60 days. However, for the remaining 3 sources, a 5-minute acid soak improved germination even when combined with the longest (60 days) stratification treatment.

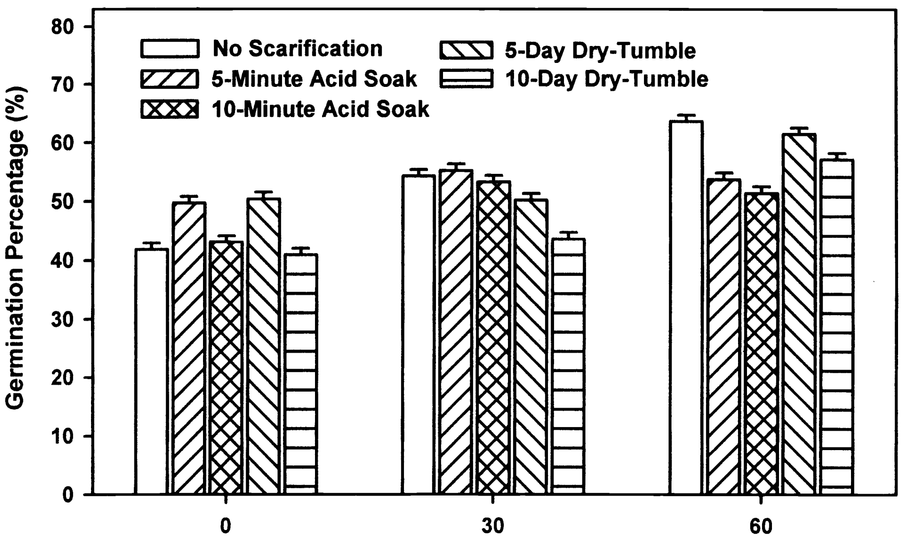

Fig. 3. Effect of interaction between stratification and scarification (averaged across seed source) on mountain mahogany germination for the 5-source experiment.

Discussion

Overall germinability and response to scarification treatments was highly variable among the New Mexico sources of mountain mahogany studied. Considerable ecotypic differences exist within mountain mahogany species (Young et al. 1978). Ecotypic and environmental differences among populations interact to affect seed dormancy (Baskin and Baskin 1973) and viability, and could account for the variability in reported stratification and scarification requirements of mountain mahogany (Hervey 1955, Heit 1970, Smith 1971, Deitschman et al. 1974, Kitchen and Meyer 1990).

Kitchen and Meyer (1990) found variability in stratification requirements of 9 Utah and Colorado mountain mahogany seed sources to be related to environmental factors such as winter precipitation and the probability of spring drought (but not elevation), in addition to winter temperature. These environmental factors may also account for some of the variability among New Mexico sources, where precipitation varies along latitudinal and elevational gradients. The data in this study suggest a latitudinal gradient in the degree of stratification requirement between northern and southern New Mexico seed sources and an elevational gradient in stratification requirement between upper and lower elevational seed sources at a single location.

Scarification treatments improved germination to a limited extent in this study. As was the case in previous studies, scarification treatments were less effective than stratification in promoting germination (Hervey 1955, Heit 1970, Smith 1971). Scarification in concentrated sulfuric acid was a more effective treatment than dry-tumble scarification for 4 of 7 sources, but for 2 seed sources, all levels of acid scarification significantly reduced germination. Variability in reported optimal acid-soak duration in mountain mahogany (Hervey 1955, Heit 1970, Dreesen, unpublished data) is likely the result of variability in seed coat thickness among seed lots. Seed coat thickness is a major factor related to both the requirement for and the sensitivity to scarification treatments.

Although acid scarification is often employed to improve seed coat permeability or soften restrictive seed coats, neither of these dormancy mechanisms is documented to occur in mountain mahogany (Heit 1970). However, mountain mahogany seeds contain a water-extractable inhibitor

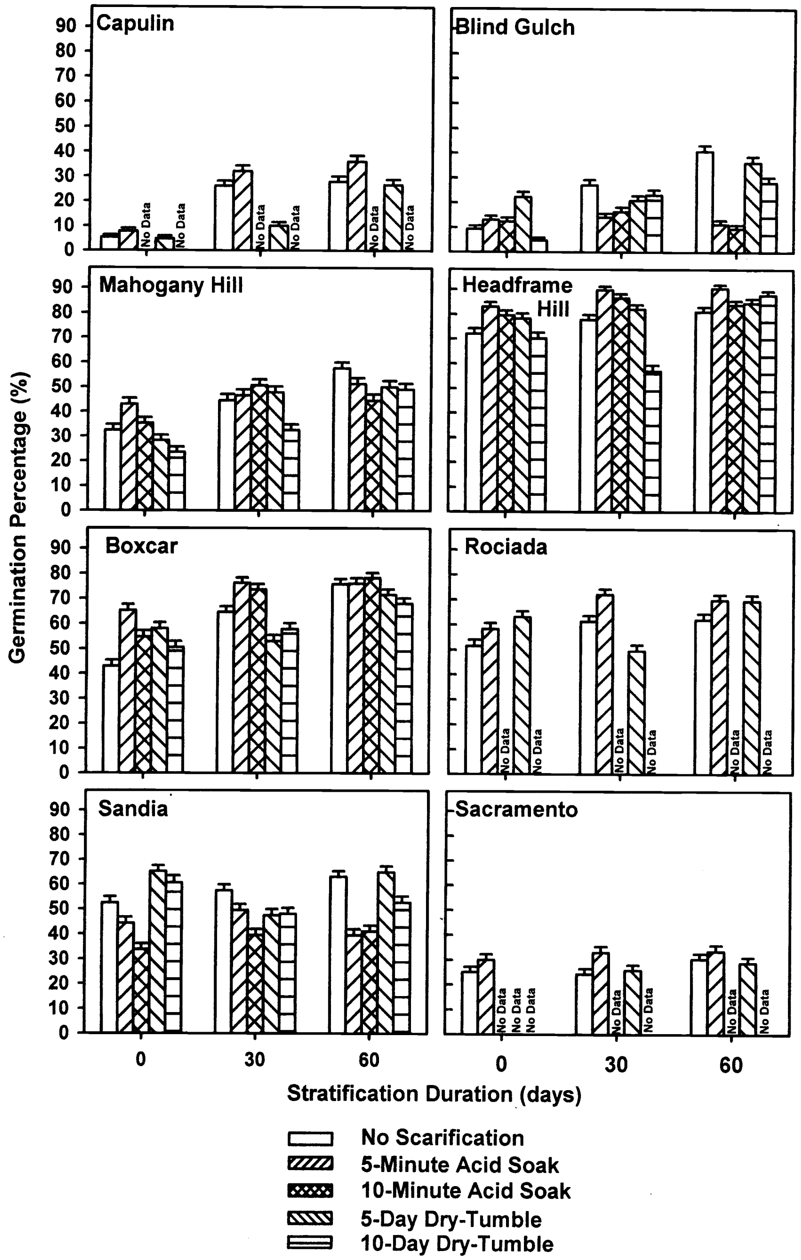

Fig. 4. Effect of interaction between seed source, stratification duration, and scarification treatment on mountain mahogany germination.

that may be hydrocyanic acid or a cyanogenic compound (Moore 1963). Acid scarification may chemically alter or remove these germination inhibitors from the seed coat. Dry-tumble scarification, on the other hand, would be expected to be less effective in reducing seed coat-inhibitor content. Variable response to acid scarification among seed sources may be explained by variablity in inhibitor content.

There was no elevational or latitudinal trend among sources in response to scarification treatments in this study. Microclimatic, edaphic, and other local biotic and abiotic factors rather than macroclimate may influence seed source response to scarification treatments. This pattern of variability contrasts sharply with variability in stratification requirement, which delineates along macroclimatic gradients.

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Book Reviews

The Politics of Precaution: Genetically Modified Crops in Developing Countries. By Robert L. Paarlberg. 2001. Johns Hopkins University Press, Baltimore and London. 180p. US$19.95. Paper. ISBN 0-8018-6823-8.

In the early 1970s, scientists—almost exclusively in the western world—began orchestrating actual recombinations of DNA molecules by moving particular genes carrying desired characteristics from a source life-form into the DNA of a living target organism. Why was this done? The answer is that in comparison with the slow and often inaccurate techniques that accompanied conventional plant breeding, recombinant DNA gave scientists a quick, more potent, and a possibly more accurate technique. This novel technique has increasingly been referred to as genetic modification or simply as GM. With the availability of these GM techniques, scientists have been able to produce a variety of agricultural plants with a number of acceptable attributes.

Given the salience of agriculture in the developed and in the developing world, the subject of genetically modified or GM crops has aroused great interest across the world. Are GM crops really the panacea that their protagonists claim they are? What are the real and hypothetical dangers associated with the planting of GM crops? Why is it that dissimilar countries have reacted so differently to the adoption of GM crops? Finally, in the context of GM crops, what lessons do we learn by studying the disparate reactions of 4 important developing countries? The general purpose of this book is to shed light on these sorts of questions. The specific "purpose of this book is to document and explain [the] emerging pattern of policy resistance to GM crops among some developing-country government authorities" (p. 4).

How does one begin a meaningful study of the policy opposition to GM crops by dissimilar developing countries? Chapter 2 proposes one way. As this chapter helpfully points out, any purposeful analysis of the above question must adequately discuss a nation's response in 5 policy areas. These areas are intellectual property rights (IPRs), biosafety, international trade, food safety and consumer choice, and finally, public research investment. Having specified these 5 areas, this chapter uses a 4-part classificatory scheme to study national responses in each of the 5 policy areas identified above. In this scheme, a country's response in each of the five areas is either promotional, permissive, precautionary, or preventive. The 4 developing countries that are studied in this book are Brazil in Latin America, China and India in Asia, and Kenya in Africa.

Governmental caution and weak capacity in Kenya is the subject of Chapter 3. As far as IPRs, biosafety, international trade, and public research investment are concerned, Kenya's policy choices have been precautionary. Only in the area of food safety and consumer choice have Kenya's policies been promotional in the sense that this nation's food safety and labeling laws have not made any distinction between GM and non-GM foods. What explains this highly precautionary state of affairs? According to this book, the "explanation for Kenya's caution can be found in its weak governmental capacity and its high dependence on the donor community" (p. 63). Although this is a plausible explanation, 2 questions arise. First, is Kenya's dependence on the international donor community excessive relative to the other countries being studied in this book? Second, what about Kenya's dependence relative to that of other African countries? Regrettably, these questions are not addressed in any significant detail in this chapter.

What about Brazil? A perusal of Chapter 4 tells us that with regard to IPRs and food safety and consumer choice, this nation's policies have been permissive. In contrast, as far as biosafety and international trade are concerned, this country's policies have been precautionary. Only in the area of public research investment have Brazil's policies been promotional. Although it is helpful to know this, my only concern here relates to the length of the author's study period. As pointed out on p. 157, the length of the study period is 1999–2001 for the other 3 countries. However, for Brazil (see p. 69) it is 1999–2000. Given the brevity of this study period, the inferences drawn in this chapter are fundamentally "snapshot" inferences. Do such inferences tell us anything substantive about the future? On a related note, why focus on Brazil specifically and not on, say, Argentina? I suspect that many readers will ask these sorts of questions.

Chapters 5 and 6 focus on the policy responses of India and China. Since these 2 populous developing countries are often compared, in this review, I shall consider the analysis of these 2 nations together. In India, IPR and international trade policies have been preventive. In contrast, in China, IPR policies have been precautionary and international trade policies have been permissive. In India, biosafety policies have been precautionary and food safety and consumer choice policies have been permissive. In contrast, in China, biosafety and food safety and consumer choice policies have both been permissive. Only in the area of public research investment have policies in India and in China been promotional.

What accounts for these differences? In India, non-governmental organizations (NGOs) have successfully fomented a number of anxieties. For instance, one NGO used "biosafety rules and procedures to try to block Bt cotton, but the core of its argument against this GM crop was that it was being introduced from abroad by the Monsanto company, which owned rights to the dreaded "terminator" technology"(p. 106). In stark contrast, in China, there is virtually no political space for independent critics to challenge state policy. As this book rightly points out, "a lack of open political space for civil society to challenge government policy in China has been one reason for China's ability to go ahead with some GM crops while others in the developing world have not" (p. 155). Therefore, this book reasons that China's "policy insulation approach should not and probably could not be imitated by others" (p. 155).

Let me conclude this review by noting that, in general, this is a topical and a well researched book. Despite a few errors of omission, this book makes a number of points that are both correct and thought provoking. Consequently, I recommend this book to all readers who wish to learn more about the ontogenesis of policies pertaining to the adoption of GM crops in 4 prominent developing countries.—*Amitrajeet A. Batabyal*, Rochester Institute of Technology, Rochester, New York.

Invasive Exotic Species in the Sonoran Region. Edited by Barbara Tellman with 29 text contributors. 2002. The University of Arizona Press and the Arizona-Sonora Desert Museum. 424 p. US$75.00 cloth. ISBN 0-8165-2178-6.

The distinctive flora and fauna of the Sonoran region inspire above average interest in the potential, ongoing and historical effects of invasive species in that landscape. And deleterious invaders, both producers and consumers, are not in short supply. In *Invasive Exotic Species in the Sonoran Region*, we are provided a broad survey of the ecology and ecological management of diverse invasive species in the Sonoran Region of the American Southwest and Northern Mexico. The book is the product of a symposium held 4 years earlier in May 1998 at the Arizona-Sonora Desert Museum near Tucson, Arizona. From my non-specialist perspective, 4 years from symposium to publication seems a leisurely publishing schedule on a topic as dynamic and virulent as invasive species, where a few years can be an eternity. In any case, among the contributors to the book are some notable regional, national and international specialists in the ecology of arid lands.

An interesting preface by Gary Paul Nabhan and informative introduction by the editor commence a text that is divided into 3 major sections. The 4 chapters of Part 1 examine invasive species from a broad perspective. Chapter 1 by Thomas Van Devender examines the history of Sonoran Region immigrations on a geological time scale. Chapter 2 by the editor explores the notably frequent and dubiously strategic introductions by humans in recent times. Chapter 3 examines the Sonoran floristic province and Chapter 4 discusses barriers to plant naturalizations and invasions.

Chapters 5 through 13 constitute Part 2, and these chapters cover a diverse group of specialized topics involving sub-regions within the Sonoran Region, particular kinds of invasive species, or special topics related to invasions. Sample topics are diverse, and include: *Invasive Vertebrates on Islands of the Sea of Cortez*; *Exotic Species in Grasslands*; *Mexican Grasslands, Thornscrub, and the Transformation of the Sonoran Desert by Invasive Exotic Buffelgrass (Pennisetum ciliare).*

Part 3 addresses exotic species management in 6 chapters, covering such topics as plant protection and quarantine, biological control, fence-line contrasts, and case studies involving control. Chapter 19 by Jeff Lovich is a summary of the symposium's major messages, and contains a strategic call to action. The book contains a brief glossary, and 3 admirable appen dices, including a summary of laws, agreements and executive orders related to exotic species, and lists of species of flora and fauna that have been introduced to the Sonoran Region. The list of cited literature in extensive; it is compiled at the end of the book rather than at the end of each chapter. A general index and brief bios of the contributors complete the book.

The contributed chapters of Dr. Tellman's edition are semi-technical in character, typical of a university press book. Some chapters, even within sections, are more specialized than others, and some are sufficiently surfeited with references that their readability is slightly impaired. Collectively, though, *Invasive Exotic Species of the Sonoran Region* is a good survey of the ecology and the issues involved with floral and faunal invasions of the Sonoran communities. It should be of interest to students, researchers, land managers, and environmentally aware citizens, especially in that region, who will surely find value in some aspects of its diverse content. – *David L. Scarnecchia,* Washington State University, Pullman, Washington.

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