Journal of Range Management

TABLE OF CONTENTS: VOL. 56, NO. 6, November 2003

FEATURE ARTICLE

Plant/Animal

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.

PRINTED IN USA

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Soils

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—to develop an understanding of range ecosystems and of the principles applicable to the management of range resources;

—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;

—to promote professional development of its members.

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J. Range Manage.
56: 558-569 November 2003

Viewpoint:
Empowering diversity: Envisioning, designing, and developing *range management science*

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Abstract

The fragmented, weak identity of range science has been disadvantageous to the institutions and individuals involved with it. This paper addresses a complex, interrelated group of issues related to range science, the *Journal of Range Management*, and the Society for Range Management. Beginning with the longstanding conception of the *art* of range management, it presents a concept of *range management science* that has multiple implications for the Society for Range Management and its flagship publication, the *Journal of Range Management*. The paper presents a strategically designed identity for range management science as a *synthetic* science, i.e., a science of *synthesis*, and examines the elements of diversity, synthesis, and communication that are the essence of that identity. It encourages a diverse, inclusive, synergistic character for, and offers many suggestions related to the philosophy and conduct of, the science, the *Journal*, and the Society. The harmonious vision of range management science that it presents is designed to give the science a strong, coherent, marketable identity. The vision is dynamic in that it can readily accommodate evolving changes. That vision is designed to make the diversity of the science and the Society work for us, rather than against us, by establishing a philosophical environment where the kind of scientific, institutional, informational, and professional synergies we need can flourish.

Key Words: synthesis, concepts, diversity, *Journal of Range Management, Rangelands,* university range programs, art

Resumen

Las diversas instituciones asociadas con la ciencia de pastizales han sufrido de la fragmentación de la ciencia e identidad débil. Este artículo aborda un grupo interrelacionado y complejo de problemas relacionados a la ciencia de pastizales, el *Journal de Manejo* de Pastizales y la Sociedad para el Manejo de Pastizales. Iniciando con la concepción largamente sostenida del arte de manejo de pastizales se presenta un concepto de ciencia de manejo de pastizales que tiene múltiples implicaciones para la Sociedad para el Manejo de Pastizales y su principal publicación, el *Journal de Manejo* de Pastizales. El articulo presenta una identidad estratégicamente diseñada para la ciencia de manejo de pastizales como una ciencia sintética, esto es, una ciencia de síntesis, y examina los elementos de diversidad, síntesis y comunicación que son la esencia de tal identidad. Motiva a un carácter diverso, incluyente y sinérgico y ofrece muchas sugerencias relacionadas con la filosofía y conducta de la ciencia, el *Journal* y la Sociedad. La visión harmoniosa de la ciencia de manejo de pastizales que el presenta esta diseñada para dar a la ciencia una identidad fuerte, coherente y vendible. La visión es dinámica de tal manera que puede fácilmente acomodar los cambios de se desarrollan. Esa visión esta diseñada para hacer que la diversidad de la ciencia y de la Sociedad trabaje para nosotros y no en contra de nosotros mediante el establecimiento de un ambiente filosófico en donde pueda florecer el tipo de sinergia científica, informacional y profesional que nosotros necesitamos.

This paper addresses a complex, interrelated group of issues related to range science and the Society for Range Management. The paper's mission is explanation of a vision of *range management science*—a comprehensive vision directed at achieving multiple objectives for the science, for the Society, and for the educational and research institutions involved with them. It presents a concept of range management science as an inclusive, integrative, *synthetic* management science of diverse kinds of *communication*.

The analyses in the paper are conducted from a perspective formulated from the following evaluations:

1. The current trend toward diversity and inclusiveness in range science, and in the membership of the Society for Range Management, have arisen naturally, i.e., *ecologically*, in a competitive environment, and so may be used as indicators of the *natural* trend in the identity of range science.
2. Diversity and inclusiveness in range science and the Society for Range Management are strengths to be fostered and utilized, not weaknesses to be diminished or circumvented.
3. The Society for Range Management currently faces significant problems, including declining membership, questions about the quality of its underlying science, and a fragmented professional vision, and these problems are not the result of a single circumstance, but are the result of an interrelated complex of circumstances.
4. These problems are better addressed by execution of a comprehensive plan that will involve professional synergies to achieve multiple objectives, and by a plan that is dynamic, i.e., that can readily accommodate inevitable future change.

The author would like to thank Drs. M. M. Kothmann and J. K. Dobrowolski for their reviews of the manuscript.

Manuscript accepted 15 Jul. 2003.

5. To be successful, any such plan will effectively use the natural diversities of the science and profession to work *for* the science and the Society by philosophically unifying them, rather than allow those diversities to work *against* the science and the Society by philosophically fragmenting them.
6. The principal function of the Society for Range Management is communication, not advocacy.
7. The character and identity of *range science* have been inadequately defined by the Society, and this inadequate definition has contributed to the Society's current limitations.

The paper begins with an analysis of past and present interpretations of the *art* and *science* of range management, and a notable early concept of range science. It then addresses the visualization of range management science. It examines the importance of communication and *art*, and the mutual importance of *identity* and *communication* to each other in range management science. The paper examines the implications of range management science for the name of the Society for Range Management. It makes specific recommendations regarding the Society's flagship publication, the *Journal of Range Management*, and evaluates the general implications of *range management science* for the Society's popular publication, *Rangelands*. It explores diverse implications of an inclusive concept of range management science for programs at the land-grant universities. The international dimensions of range management science are examined. The paper returns to another aspect of communication with a discussion of the challenge facing the next incarnation of the committee to revise the *Glossary of Terms Used in Range Management.*

Throughout its development, the paper emphasizes the importance of a broad concept of *synthesis* in range management science, expanding or generalizing elements of synthesis that are discussed or exemplified in 4 other papers (Scarnecchia 2004a, 2004b, 2004c, 2004d). Along the way, the paper makes many suggestions, but adoption of a diverse, inclusive, integrative concept of range management science is explicit or implicit in all of them.

Range Science and Range Management

The problem of identification of range science can be traced back to historically frequent and sometimes lengthy philosophical discussions about the distinctions between *art* and *science*, and between *range science* and *range management.* The question of the relationship between *range science* and *range management* has been considered many times in published work (e.g., Provenza 1991), at professional meetings, and in classrooms. I am unsure about the *published* origin of the term *range science*, but among the most conspicuous early uses of the term is that in the third edition of *Range Management* (Stoddart et al. 1975). The term was absent from the second edition (Stoddart and Smith 1955). *Range science* was not explicitly defined in the third edition, but was defined graphically in Figure 1, which is reproduced here.

Examining Figure 1, *range science* was represented as a central science that drew on a number of other specialized sciences, including ecology, soils, sociology, etc. Each of these specialized sciences contributed to range science, contributing to the band inside of these basic sciences (Fig. 1), i.e., to the outside band of what was represented as *range science.* The band itself, presumably, consisted of specialized sub-sciences within range science, e.g., range ecology, range economics, range wildlife biology, etc. Whatever its origin, and whatever the intentions of its designer, Figure 1 begs an obvious question; *what is in the (curiously large) core of range science?*

You will not find much in the published literature that attempts to answer this question, other than several papers from the middle and late 1990's (e.g., Scarnecchia, 1995a, 1996, 1999). In fact, 25 years after the publication of Figure 1, the most widely used current textbook in range management (Holechek et al. 2004) has only a single brief paragraph of 6 sentences on *range science*, and following the definition of Provenza (1991), defines it as "the organized body of knowledge upon which range management is based." Figure 2, taken from that book, clearly does not answer the foregoing question about the identity of range science. In fact, examining Figure 2, range science is not even in the figure. Where is it? Why does it not have the standing of the other sciences shown in Figure 2? And why is a whole generation of university students taking courses in range management without being given a clear vision, beyond 6 sentences, of what range science is? Twenty-five years later, in the roll call of sciences in Figure 2, range science has, with more than a touch of paradox and irony, *turned up missing.*

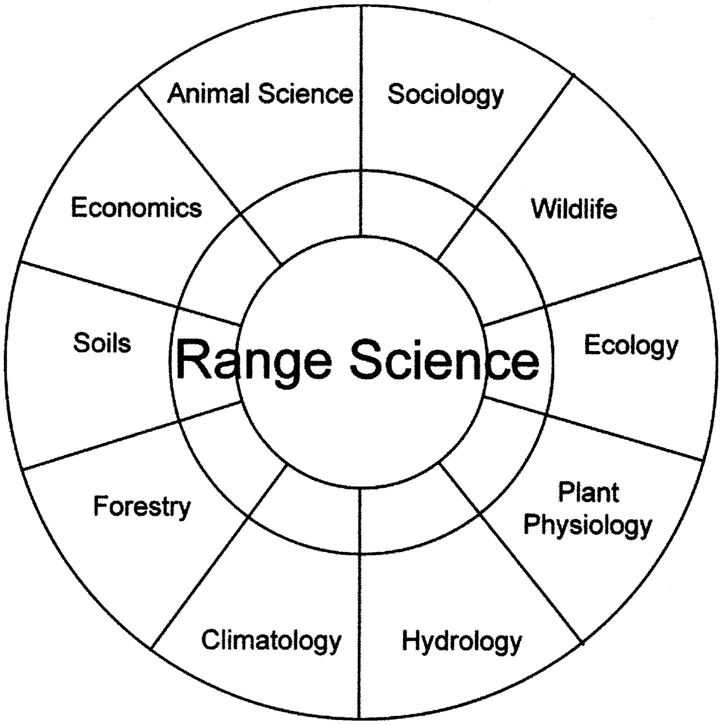

Fig. 1. Range science as conceived in the major textbook on range management in 1975 (Stoddart et al. 1975). Neither the figure nor the book's text suggests the nature of the central core, or the band surrounding the core, although both are considered within *range science.* (Reprinted by permission of The McGraw-Hill Companies, Two Penn Plaza, New York, N.Y.)

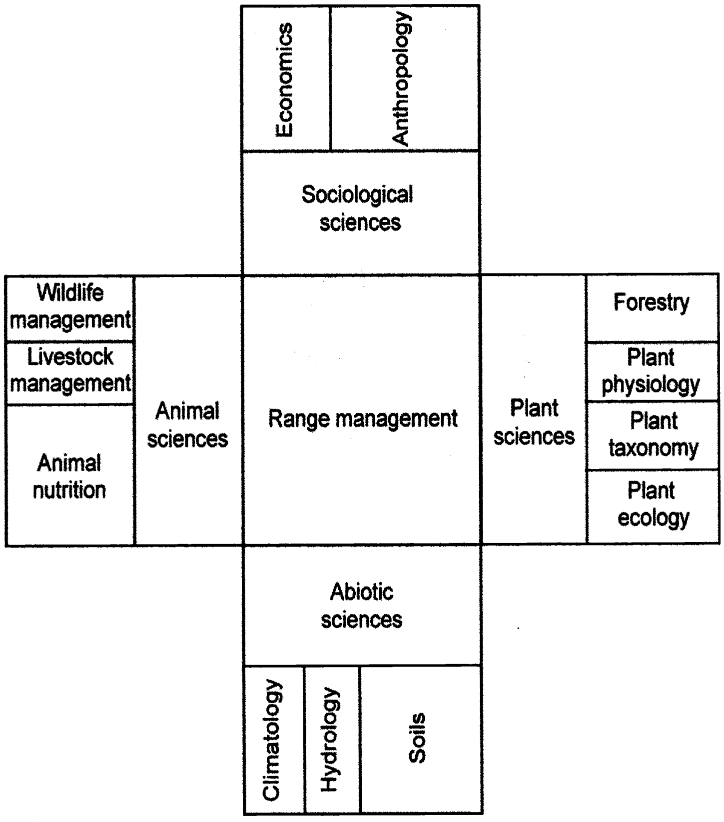

Fig. 2. Range management as envisioned in the major textbook on range management in 2004 (Holechek et al. 2004). Range science's absence in noteworthy, as is its minimal description in the book's text. (Reprinted or electronically reproduced by permission of Pearson Education, Inc., Upper Saddle River, N.J.)

An Identity for Range Science – Choosing Strategically

Notwithstanding the 3 papers related to range science cited above, the absence of range science in Figure 2 implies convincingly that the science has not developed a strong individual identity. The problem is not limited to range management textbooks. The several incarnations of the committee to work on the *Glossary of Terms Used in Range Management*, have, in my view, given insufficient emphasis to terminology describing what range science is. If a science, a discipline, or their working professionals cannot be concisely identified, they have identity problems.

Some see the core of range science as being, for example, range ecology. If the designer of Figure 1 had envisioned one of the disciplinary sciences, e.g., range ecology, as the core of range science, Figure 1 would have been drawn like Figure 3. Although ecological systems, and the concepts of ecological science have great importance in range science, the science of ecology, and its sub-sciences (e.g., terrestrial ecology, arid land ecology, aquatic ecology, riparian ecology) have long-established identities and institutions that leave little room for range ecology as a strong core for range science. Despite the long history of contributions of ecology to range science, the science has yet to find a distinct identity in, or as, range ecology. And as noted in earlier writing (Scarnecchia 1995b), even though most know that the Greek root of ecology, *oikos*, means *home*, range science is unlikely to find a comfortable professional home there.

The failure to develop a distinct identity for *range science* has contributed significantly to the recent and ongoing political and financial misfortunes of *range management*. As a starting point to improve our fortunes—for the academic institutions involved with range science, for the identities of the *Journal of Range Management* and *Rangelands*, and for expanded future success of the Society for Range Management—we need to establish a viable, functional identity for range science.

Management Science and Range Management Science

The term *management science* is used here in a broad sense to mean *an integrated science of concepts, experimental research, and analytical approaches designed, organized and oriented at management.* Important earlier works describ-

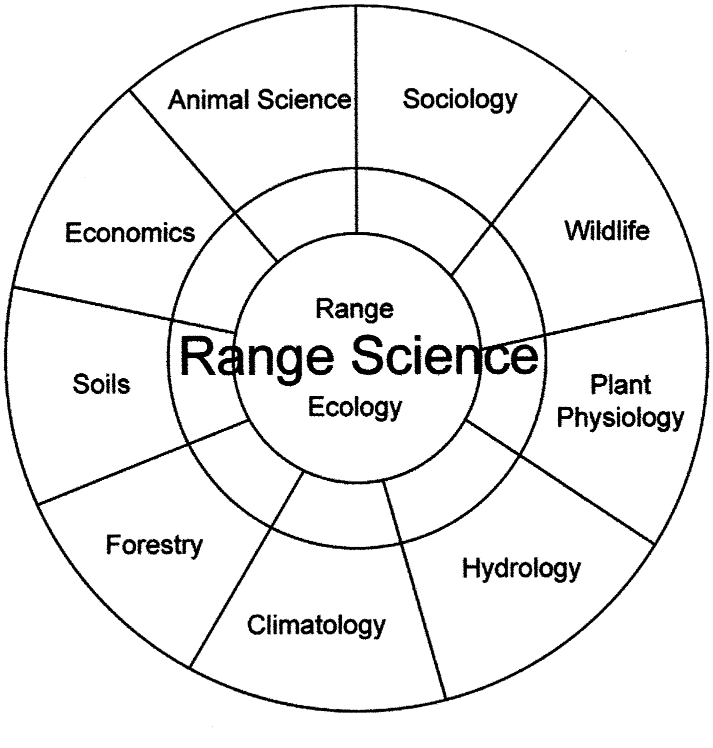

Fig. 3. Range science as represented in Figure 1, with range ecology at the core. As a technical, specialized sub-science, range ecology makes a poor center or *core* for range science.

ing management science (e.g., Forrester 1961) and more recent ones (e.g., Gass and Harris 1996) have not always concisely or explicitly defined *management science*, but historically the term has often been tied to the more narrowly conceived *operations research*, and to a complex of analytical (modeling) techniques directed at optimization problems. Specialized scientists may tend to view the concepts above, including *management science*, narrowly, but virtually all problems in science and management involve optimization.

Management science has been successfully established as an analytical science, and some modeling tools have been applied to problems of rangelands or range management. But management science elements, including concepts, tools and terminology have seldom or only slowly been effectively integrated into mainstream range science. The more technically developed sciences of wildlife biology, animal sciences, and forestry have likewise been notably ineffective in integrating elements of management science into their scientific cores, but their longer histories, their associations with higher-value products, and their better-established constituencies have allowed them to maintain their scientific integrities and identities more successfully than has range science (Scarnecchia 1995a).

Figure 1 is a useful place to start in defining range science not as a specialized basic science, but as an inclusive, integrative management science, i.e., as *range management science*. The essential features of Figure 1 were accentuated in Figure 4, reproduced from Scarnecchia (1995a), and are further refined in Figure 5. As a *model*, range science becomes a management science that includes a mantle consisting of elements of other sciences that contribute to it (Fig. 5). The mantle area of Figure 5 represents where most of the research that has been done by individuals who define themselves as range ecologists, range hydrologists, range plant physiologists, range animal nutritionists, etc., is located. Some of the research in the mantle has historically been theoretical, involving, for example, ecological theories, but most has been experimental, involving data.

Interestingly, if we consider a *range management science* as represented in Figure 5, the problems of identification disappear. The representation of range management science in Figure 5 is patterned after Earth, but unlike Earth, whose core is mostly highly tangible *iron*, the *core* of range management science is an amorphous, undifferentiated mass. Actually, to think of it originally having been, and still largely as, a kind of primordial, (albeit conceptual) unsynthesized *ooze* analogous to that described by Loren Eiseley in *The Immense Journey* (1959) is metaphorically accurate, and immensely useful. Just as higher forms of life arose from primordial ooze through some manner of *evolutionary synthesis*, the primordial core of range management science must be synthesized into a management science of useful concepts—concepts abstracted to varying degrees and useful in communication of many kinds. ***At its core, range management science is a synthetic science—a product of synthesis.***

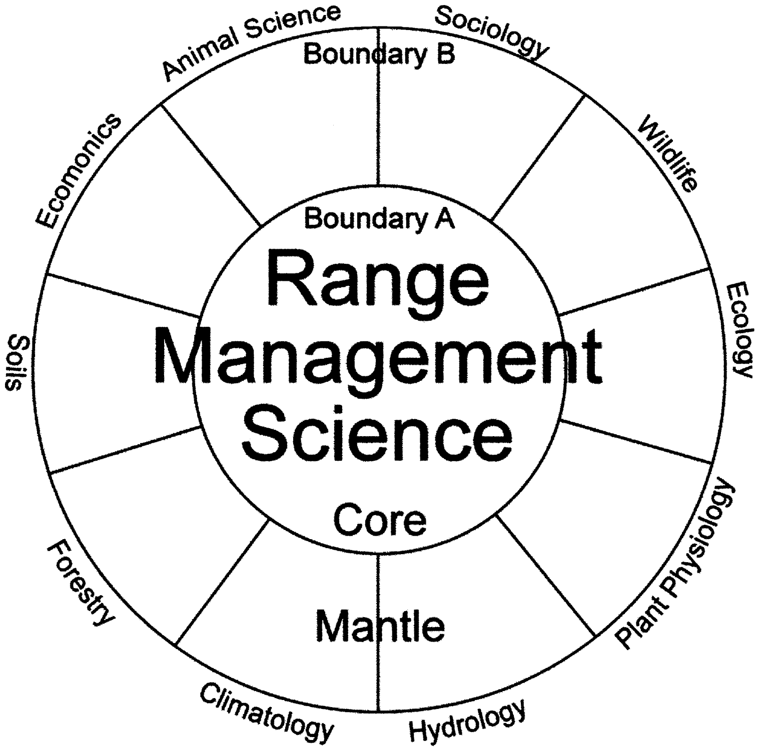

Fig. 4. Range science as *range management science*, as adapted from an earlier paper by Scarnecchia (1995a). The *core* of range management science was envisioned to consist of diverse, designed, abstract concepts, from simple basic variables to complex integrative concepts like rangeland condition or health.

Synthesis, Art, and Range Management Science

Such an abstract, conceptual vision of range management science as a science of synthesis is not incompatible with the *reality* of rangeland. In his book *Synergetics*, Buckminster Fuller (1975) wrote: *The artist was right all the time; nature is conceptual.* That statement has philosophical merit, because our concept of nature is, by definition, conceptual. But pragmatically, to consider range management science as a model, as designed, as manmade, as conceptual, is extraordinarily useful. The design of tools to investigate, analyze, explain and communicate is the *synthesis* that defines a unique science, and the diverse manifestations of that synthesis will give range management science a distinct identity.

For that reason, *art* and *design* are included as important contributors to range management science (Fig. 5). The segments representing the basic sciences are of differing widths, representing the idea that some sciences, such as ecology, contribute more content to range management science, and others may have potential to contribute more. The relative widths of these slices change over time as the relative influences of these contributing sciences change. The 3 sets of dotted slices in that figure are left mostly unnamed in anticipation that still other sciences or *branch sciences* may contribute to the development of range management science in ways that are currently unrecognized or unanticipated. As an inclusive, integrative management science, range management science should be open and receptive to these creative contributions

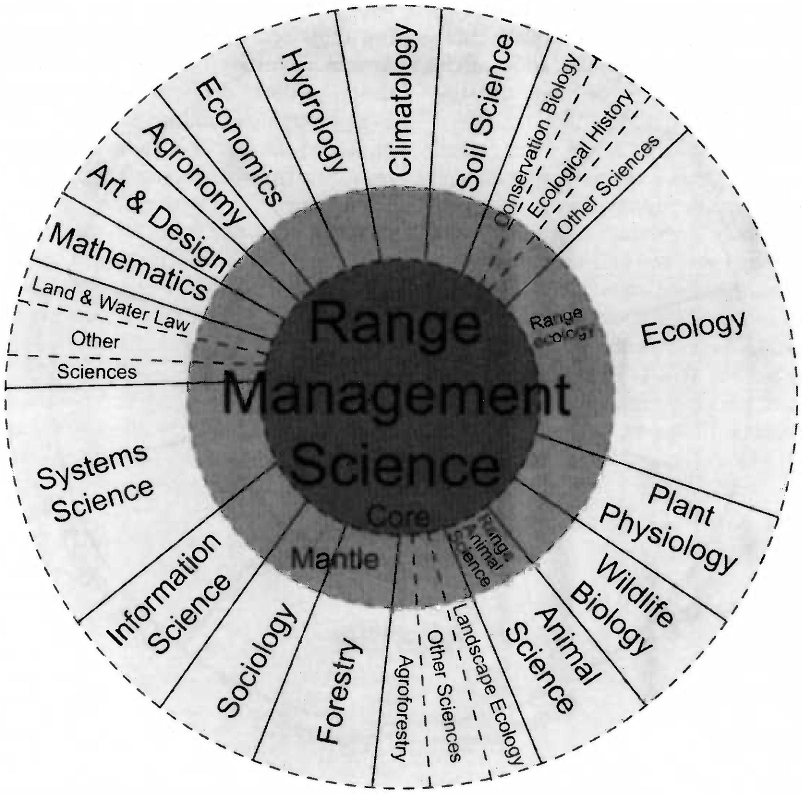

Fig. 5. Range management science as the diverse, integrative management science envisioned in this paper. The figure is dynamic in several senses. Information can flow inward from the specialized sciences to range management science, or outward from range management sciences to the specialized sciences. The relative importance of contributions of the various specialized sciences to range management science will change over time. Also, individual identities of the sciences and sub-sciences can change. Both the figure, and the management science it represents, are designed to accommodate these dynamics.

from other developing basic or applied sciences.

Although less *tangible*, the identity of range management science as the integrative management science represented in Figure 5 is a more powerful identity than any identity tied to a particular specialized science like ecology, or an identity tied simply to *rangeland*. As a latter-day science, range science has been notably ineffective in establishing a viable identity partly because specialized sciences from ecology to forestry to wildlife biology to agricultural economics to rural sociology have usurped the specialized identities, ecosystem components, and valuable products by prior claim. In simple terms, if we concede the wildlife to the wildlife biologists, the water to the hydrologists, the trees to the foresters, the plant communities to the plant ecologists, the domestic livestock to the animal scientists, the people and their communities to the rural sociologists, etc., range scientists have little to investigate, and range managers little to manage. Conspicuously few high-value products or specialized processes of ecosystems remain.

But the potential to *synthesize*—to design concepts, develop interactive approaches, pursue multiple efficiencies, and package information to communicate among the more specialized sciences is enormous. As an interactive, integrative, management science of synthesis, and of communication of many kinds, range management science is not crowded into a specialized competitive niche of low-value products or specialized processes, but instead has all of the scientific space of the open range.

The idea of range science as a management science is not without historical origins. For example, definitions of rangeland have usually been based on the kind of management applied to land rather than to specific, physical characteristics of the land. Furthermore, the idea that the essence of range management science is a *synthetic* science—a science of *synthesis*—should not seem radical. Philosophically, it is a formalization of the long established (e.g., Stoddart and Smith 1943) concept of range management as an integrative *art*. Some of our more complex concepts in range management science, including *range condition, range health, carrying capacity* and *range readiness* have widely recognized, *implicit* images in the history of what has frequently been termed the *art of range management*, even if their *explicit* identities in range science have developed only grudgingly. Such *art* has long been considered a significant part of range management, even if *art* was sometimes interpreted vaguely, only as a kind of integrated judgment that transcended limitations in quantifiable science.

But art was not explicitly present in the early conceptions of range science (see Fig. 1), and art is not commonly considered a significant component of any of the specialized sciences contributing to range science in Figure 1. Somehow we have not pursued the observations of Forrester (1961) that *as the science grows, it allows further extension of the art.* Ironically, had we, over the past 50 years, pursued the technical essence of the *art* of range management with the analytical fervor that we have pursued the *science*, range management *science* would have been better identified and further advanced than it is today. In any case, a management science philosophy does not dispense with art; it includes art; it welcomes art; and it fosters art by providing an environment in which we can pursue creative synthesis.

This paper does not suggest that we reduce our interest in experimental research or experimental science. It does suggest that we increase our attention to *synthesis*, that we recognize diverse analytical research, including modeling research, as essential research within range management science, and that we correctly visualize the role of experimental science within the broader structure in an integrative range management science.

A Science of Communication

To accomplish synthesis, organization is essential, as is communication. In fact, whether defining a basic concept like an *animal-unit* (Scarnecchia and Gaskins 1987), applying an ecological theory in assessing range health, explaining a scientific principle to a manager, or solving a multi-variable problem involving multiple human objectives or multiple efficiencies, in its functional synthetic core, ***range management science is almost entirely a science of communication.*** Much more than being simply applied ecology, land management or people management, it is a management science that should be designed to investigate, analyze, integrate, and communicate multiple objectives, variables, interactions, values, and behaviors of complex systems, that involve, broadly, *rangeland*. The land that it is directed at managing is *real* and *natural*. But the synthetic core of range management science is *abstract, conceptual*, and *man-made*.

An example of a problem in range management science is that of assessing *rangeland health*, a more comprehensive, multiple-objective conceptual expansion of assessment models that have historically been termed *rangeland condition* and *rangeland trend*. Much of the attention directed at this problem in recent years has focused on what ecological model of plant community succession is superior, e.g., traditional Clementsian succession or a state-transition model. Conceptually, this argument about ecological models is within the mantle of range management science (Fig. 2); the argument over the general validity or *at hoc* appropriateness of ecological theories or ecological models, important though it may be, is clearly central to ecology.

The challenge within the core of range management science is to develop a generalized model of values, concepts, variables and sampling protocols to apply appropriate models in appropriate locations on appropriate and diverse scales. Any model that does these things involves much more than just rangeland; it involves, among other elements, other specialized sciences (Fig 5), human values, several kinds of communication, and skillful, organized, integrated design. In that sense, the term range*land* health is too narrow to fully describe the diverse elements involved. In any case, when an individual or committee attempts to develop such a model of rangeland health, consideration of the relative validities of different ecological models is a relatively small part of the process.

Ideally, a general rangeland health model should be designed with a modular structure so that submodels, such as particular models of ecological succession, could be applied selectively where appropriate, by a generalized model of rangeland health (Scarnecchia 1995a). Whether universal or local in application, a rangeland health model should be designed to apply, interpret, translate, and in at least those 3 senses, *communicate* information about the health of rangeland to individuals concerned with management. The ecological models are models central to ecology, but the rangeland health model, with multiple objectives, multiple values, and indicator variables, compares ecological conditions with an ecological model on appropriate spatial and temporal scales, and is essentially a communication model within the core (Fig. 5) of range management science.

The visualization of range management science as a science of communication is timely in an age when accurate, useful information is becoming a more valuable product than ever, and *information science*, or *informatics* is flourishing. Much of modern informatics is concerned with the function of communicating valid information in a form that is useful for making decisions, and the variables, interactions, and models of that function are part of the core of range management science.

Another Kind of Communication

What we have here is a failure to communicate...

-- From the Film *Cool Hand Luke.*

If you think *range management* and *range science* do not have identity problems at the academic level, you are not listening to the hesitant words of your colleagues or mentors when they are asked what they do for a living.

Ask around. By that I mean, the next time you are sitting at a table of scientists in the ecological, natural resource, or agricultural sciences, ask them to give their name and to identify their discipline. Agricultural economists will say they are agricultural economists. Wildlife biologists will say that they are wildlife biologists. Plant ecologists will tell you they are plant ecologists.

Most professionals associated with range management science will, in my experience, start squirming. Few seem comfortable calling themselves *range scientists*, maybe because many do not see themselves as *real* scientists in the sense of a chemist, an ecologist, an experimental physicist, or other specialized scientist.

They will answer in one of several ways. The fortunate few who have strong scientific ties to one of the specialized sciences supporting range management science will answer with the likes of: *I'm a range ecologist, range hydrologist, range animal nutritionist,* etc. All of these specialties are, according to Figure 5, in the mantle of range management science.

The less fortunate others who are more generalist in their expertise will answer in 1 of 2 ways. Some will say, usually with some discomfort, that they are in *range management*, but this answer is unsatisfying for 2 reasons. First, most probably realize that they do not work in actual management, but instead work mostly with *concepts* and *data*. They are managing their research programs, not *range*. That reason may be why few would ever describe themselves as *range managers*, even though they admit to being *in range management*. Second, most academics are less comfortable being identified with management than with science anyway; at tables in meetings at universities, in academia generally, managers do not have the credibility that scientists do. In academia, professional peers do not always recognize people in management disciplines as *real* scientists.

Disciplinary discomfort with the word *management* leads to the third kind of response to the question of discipline. People will sometimes answer that they are *in range*, or are *a range person*, or a *range type*. I am sure you have heard individuals describe themselves or others in these terms. These vacuous, vague references, besides being symptomatic of the individual's lack of identity, erode the identity of range management science. Such references are more insidious than harmless; they perpetuate professional anonymity, even as they conjure narrow, exclusionary imagery of what, for example, a *range type* is.

In a recent *Trail Boss News* article, Vavra (2003) described the inadequate definition of "range management," expressed concern over the narrowness of "a considerable number" of peoples' definitions of range management, noted the virtual absence of Forest Service personnel who are classified as "range scientists," but concluded that "what we call ourselves (wildlife biologist, hydrologist, animal nutritionist, habitat biologist) is unimportant; the important thing is SRM provides a common forum for people interested in managing natural resources. I think we are unique in being a truly multidisciplinary society. We need to market that reality concept."

While he states (Vavra 2003) that he "never took a course in marketing," I expect that he would acknowledge the measurably greater difficulty in effectively marketing a discipline, a Society, a scientific journal, and their individual professionals without concise, coherent nomenclature to market. Clearly, we will benefit from precise, coherent nomenclature to describe a discipline, a Society, a journal, and the professionals involved with them.

One of the advantages of adopting the concept of an integrative *range management science* as described here is that professionals involved with range management science can be easily named.

Referring to Figure 5, scientists who consider themselves range ecologists, range hydrologists, range economists, etc. can retain these identities and still be range management scientists within the mantle of Figure 5. Some of these individuals who do not want to be known as specialists, and other scientists working in integrative or generalist aspects of range management science, can find identity in the core, and can refer to themselves as simply *range management scientists.*

The other professionals that contribute to range management science are technical personnel, sometimes referred to as *technical specialists* (Fuhlendorf et al. 1999). They apply range management science in their work. But historically, due to the poor development of range management science, and the complexity of problems in range management, few of these people have been involved strictly with the implementation of active management. At some time, most of them design concepts, conduct analyses, create *ad hoc* approaches or protocols, or develop other creative, *synthetic* tools that may contribute to range management science. Coordinated Resource Management is one of many examples of such approaches. Even cursory examination of the program at the recent meeting of the Society for Range Management in Casper, Wyo. clearly shows the enormous diversity and depth of ongoing and potential contributions of these technical professionals to range management science.

But because range management science as described here is not specialized in the traditional (narrow, and sometimes *grazing*) sense, the term *range management specialist* is sub-optimally descriptive. The term *range management technician* better describes the role that these professionals have in designing, modifying, and applying the *technical* information of range management science.

The Society for Range Management has shown little leadership in assigning, and little discipline in applying, appropriate titles to its professionals. Instead, universities, the USDA-ARS, and agencies like the Natural Resource Conservation Service, Forest Service, and Bureau of Land Management have filled this role and provided names, often derived from titles of position descriptions within their bureaucracies. The result has been not only fragmentation in the names used, but also the appearance and persistence of names like *range conservationist.* Not only are such titles not especially descriptive, they sometimes imply advocacy, even where none may exist. Furthermore, unfortunate slang variations of them (e.g., *range con*) can sound more criminal than professional. The Society for Range Management needs to lead in the identification and naming of the different categories of professionals involved with range management science. Then professionals like *range management technicians* will be able to clearly enunciate their professional identities with appropriate precision, and convey, in this case, the appropriate kind of *conviction.*

Adoption of the name *range ecologist* to replace *range conservationist* (the usual U. S. Office of Personnel Management title) would stretch the interpretation of the word *ecology* to the limits of elasticity. Concise descriptions of most range professionals' diverse activities include mostly the development of *management science*, or its implementation, i.e., *management.* Few of the activities of most *range management scientists* or *range management technicians* involve work within the traditional, mainstream context of *ecology.* Few scientists who recognize themselves as *range ecologists* would be likely to recognize management designs, plans, and their implementations as *range ecology.*

Changing the names of what are *range management scientists* and *range management technicians* to professional *range ecologists* would be another manifestation of range science's disciplinary retreat to the misperceived *safe haven* of ecology. Such a stretched, inaccurate name for technical professionals is unwarranted and unnecessary; the names *range management scientist* and *range management technician* are not nominally stretched, and are more descriptive of what most of these professionals actually do.

Implications for the Society for Range Management

Visualization of a range management science as described above, and as represented in Figure 5, has a number of other implications for the Society for Range Management, for its publications, and for its members. First, the name *Society for Range Management* is entirely compatible with this concept of range management science (as is *International* Society for Range Management, as discussed later in this paper). A major component of the Society's mission is encouraging informed, effective management of *range.* And while the word *range* carries significant historical, political baggage, the term is inherently and effectively broad in interpretation. Two of our challenges, ones we had better not fail in achieving, will be to *foster* and *communicate* this breadth in the interpretation of what we mean by *range.*

Recently, some university programs in *range science* or *range management* have attempted to strengthen their identities by changing the names of their departments or programs, often by adopting names including the word *rangeland*, e.g., *rangeland ecology.* As has been discussed previously, tying the core identity of range science to land, to *rangeland*, no matter how intuitively comforting that may seem, is narrowing and counterproductive. Range management science needs to imply and involve much more than simply the management of *land.* In fact, the name *rangeland management*, or the Society for Range*land* Management, would be less compatible with range management science, because the management science is synthetic; it involves many other elements than just land. We need to be counter-intuitive in this regard, and realize that even though land management may be a major goal, *concepts* make better building blocks for range management science than *land* does. If we can improve our identity and communication, and build an inclusive, integrative, creative management science, we have a better chance to overcome any current disadvantages of the word *range*, and make the word *range* work for us rather than against us. Then the *Society for Range Management* will remain a good name.

Implications for the *Journal of Range Management*

The name of the Society for Range Management's scientific journal, the *Journal of Range Management*, can be made more accurate, and more descriptive. If we adopt a simple semantic interpretation of *range management*, and define it as the actual, physical application, implementation, execution, etc, of range management science, then the *Journal of Range Management* is actually a *journal of range management science.* No actual range management (as defined above) is found there; it is all range management science.

Besides such technical accuracy, the name *Journal of Range Management Science* has other advantages. First, inclusion of the word *science* adds scientific credibility. Second, retention of the word *management* identifies it as a source of ideas to managers. Third, the compound phrase *management science* describes a diverse, inclusive, integrative science, and projects an image somehow broader than the image of *range management.* We should seriously consider renaming the *Journal of Range Management* the *Journal of Range Management Science.*

Adoption of an inclusive concept of range management science and an inclusive *Journal of Range Management Science* has other potential advantages. The current publishing environment in the specialized sciences, particular in ecology, has become highly competitive (Society for Range Management Task Force on the Journal of Range Management 2003). Because of the combined presence of older, more prestigious journals like *Ecology*, and well-established newer journals like *The Journal of Arid Environments* and *Arid Land Research and Management*, the *Journal of Range Management* will be unlikely to be the dominant publishing outlet in rangeland ecology or arid land ecology. The fact that the expansive editorial boards of these journals are peppered with researchers who might be considered important range ecologists further supports this observation. In the scholarly environment of ecology where publishing prestige is at a premium, we are unrealistic to expect that the *Journal of Range Management* can be the preferred outlet for most rangeland ecologists. Because of that expectation, we should not orient the *Journal of Range Management* predominantly as a journal of rangeland ecology.

Instead, we need a more inclusive editorial philosophy to attract as much high-quality research relevant to range management science as we can. Range ecology, especially experimental research and conceptual research that involve the kind of integration, communication and synthesis involved in the mantle and core (Fig. 5) of range management science, should continue to be a major component of that research.

Orientation as a journal of an inclusive management science would place a *Journal of Range Management Science* in an environment of less direct competition with specialized journals. The greater diversity of possible contributions would welcome other scientists into the Society for Range Management, including international scientists, domestic scientists who are not in the traditional specialized sciences represented in Figure 1, but who could make significant contributions to range management science (Fig. 5).

Identifying the Journal as an inclusive *Journal of Range Management Science* would increase demands on the editorial board of the Journal. A greater number and diversity of associate editors will be needed, including ones oriented toward international research, diverse specialized sciences (Fig 5), and management science, including modeling. Because working with a management science philosophy that will encourage creativity and *synthesis,* the technical editor, with the assistance of the associate editors, will need to be diligent in the pursuit of objective research, and vigilant to avoid publishing both pseudo-scientific advocacy and management case studies that might be semi-disguised as management science.

In an age of cooperative research, the lines are increasingly blurred between scientists and advocates, and such pseudoscience of dogma and demonstration are often the product of admirable cooperation. Cooperative organization of research can contribute to the development of management science, but some activities, such as simply gathering statistical data (Forrester 1961), or pseudo-scientific advocacy, contribute little of value to the *management science*. Science produced by research coalitions that may involve advocacy groups or individuals cooperating with poorly funded but nominally objective scientists will need increasingly careful editorial scrutiny.

Internal or External Publishing

Under a management science philosophy, the technical editor will need to give more attention to matters of mission, scope and quality however the Journal is published. If the Society for Range Management continues to publish its journal internally, the increased demands on the technical editor of a *Journal of Range Management Science* should be recognized by the Society with increased technical support and increased remuneration.

Any move to outside (joint) publishing would be likely to significantly change the role of the technical editor of the *Journal.* External publishing would reduce the editor's peripheral responsibilities in publishing, including matters of proofreading, formatting, etc., and redirect attention to defining the mission and scope of the *Journal.* Also, the technical editor would have more time to work with associate editors in improving the technical and literary quality of manuscripts.

A New Journal?

In the June, 2003 issue of *Rangelands*, the Society for Range Management Task Force on the *Journal of Range Management* (2003), based on an analysis of trends in published papers in the Journal, recommended exploration of a number of options, including consideration of a new journal of rangeland ecology. My analysis of that report (Scarnecchia 2003) in the August issue of *Rangelands* questioned the merit and interpretation of the Task Force's analysis, and contained an abridged version of the following analysis of why a second journal, one focused on rangeland ecology, seems at this time an inadvisable plan to pursue.

First, the new journal would be entering the highly competitive publishing environment of ecology described previously. In that environment, the new journal is not guaranteed to be an economic success.

Second, a new journal with an ecological emphasis would leave the current journal with strongly unbalanced content inconsistent with the diverse, inclusive management science philosophy espoused in this paper. The residual journal, with range ecology excised, is not guaranteed to be an economic success. If decreasing numbers of range ecology papers in the *Journal of Range Management* is a developing problem (Society for Range Management Task Force Report on the *Journal of Range Management* 2003), then their complete removal into a separate range ecology journal would be an acute problem.

Third, the current *Journal of Range Management* may be in need of an overhaul (in its identity, charges, subscription rates, delivery system, etc.), but notwithstanding some of the observations in the report of the Society for Range Management Task Force on the *Journal of Range Management* (2003), it is not "broken," at least not *financially*. In fact, financially, it is alive and reasonably well. Its profitability helps support other activities of the Society for Range Management. Dissecting a living organism seems unwise.

Fourth, although the *Journal of Range Management,* at least according to the interpretation of the report of the Society for Range Management Task Force on the *Journal of Range Management* (2003), has become more agricultural in its content, the lack of diversity in content created by a new journal of rangeland ecology would virtually force the original journal to publish entirely in the area of agriculture and grazing management, and thereby into becoming a journal of tacit advocacy. Any attempt to strengthen its content or finances by hybridizing the remaining journal with *Rangelands* would exacerbate this problem. In the current political environment, with *Rangelands* or without it, the remaining journal, with its unbalanced content, could not operate as a credible, objective, scientific journal if it were associated with advocacy, either explicit or tacit.

Fifth, the tacit advocacy would continue to undermine the reputation of the Society for Range Management as a source of diverse, objective, explicit range management science. In the process, it ironically would indirectly undermine the credibility of any new journal of *rangeland ecology* or *rangeland science*, because that new journal would be a sibling publication of a *journal of tacit advocacy*, with both being published by a *society of tacit advocacy*. In fact, scientists publishing in the new journal would likely be among the first to recognize and announce the unscientific character of the *management* journal. With its diverse membership, the Society for Range Management should pursue unstructured diversity in its scientific publishing in pursuit of scientific integrity and in its avoidance of advocacy.

Sixth, an *ad hoc* decision to add another journal would, unless the publication frequency of both journals were reduced significantly, overwhelm the current staff and strongly compel the Society into external publishing. Any decision regarding continuing internal publishing or initiating external publishing should be made as part of a proactive comprehensive plan, rather than as an *ad hoc* or reactive decision.

Seventh, and most fundamentally, creating a new *Journal of Rangeland Ecology* or *Rangeland Science* would perpetuate our failure to synthesize an inclusive, integrative range management science needed by the Society for Range Management, and by the institutions that contribute to it. Creation of the new journal would not address the broader problems of the Society and those institutions; it would not address the elements of *identity* and *inclusiveness* that the development of a single *Journal of Range Management Science* would address.

As part of a comprehensive publication plan, pursuit of a new, more specialized ecological journal as a companion journal to a *Journal of Range Management Science* remains a future possibility once the identity of range management science, and a Journal bearing that name, are more firmly established. But whatever the character or timing of future decisions, range ecology should continue to be a major contributor to range management science (Fig. 5), and to a *Journal of Range Management Science*.

The absence of local or regional experimental, agricultural research that involves little synthesis and has no apparent, general value to range management science would effectively strengthen a *Journal of Range Management Science*. Relocation of papers describing such research into a joint publication involving other agricultural institutions would allow elimination of them from a *Journal of Range Management Science*, and leave *Rangelands* free to pursue more creative contributions.

Implications of Range Management Science for Rangelands

The potential for creativity and communication through *Rangelands* should be significantly enhanced by a publishing philosophy based on *range management science*, and by a *Journal of Range Management Science*, because the inclusiveness of a management science philosophy should give *Rangelands* a greater diversity of contributions to publish. *Rangelands* has an essential role within the expanded concept of communication that this paper implores, including communication among range management scientists, range management technicians, and readers interested in the activities surrounding rangelands. The increased inclusiveness of the management science philosophy should invite contributions from non-traditional authors, from non-traditional disciplines, and allow upgrading of the technical and literary quality of *Rangelands*.

As a non-technical or semi-technical publication of the Society for Range Management, *Rangelands* should not indulge in the unbalanced pro-grazing advocacy of the magazine *Range*, or any overstated anti-grazing or pro-grazing advocacy of politically extreme publications. *Rangelands*, like a *Journal of Range Management Science*, should be characterized by unstructured diversity in its pursuit and communication of meritorious information, and should be vigilant in avoiding scientifically unjustifiable positions of advocacy.

Implications of Range Management Science for Programs at Universities

The American universities are likely to be hugely important in the future of range management science as an identifiable science, and in the perpetuation of the Society for Range Management, for at least the following reasons.

First, research scientists at universities, including the land-grant universities, have historically been important contributors to innovation in range management science. The interdisciplinary environments of universities both employ and educate personnel for the kind of interdisciplinary working groups that can pursue the integrative designs in the core of range management science.

Second, the universities have historically been recognized as the institutions most likely to conduct objective research. Notwithstanding recent and ongoing deterioration in independent, hard money funding for research at these institutions, they still promise to be important sources of objective research. The Society for Range Management and a *Journal of Range Management Science* must have and promote such objective research if they are to pursue *objective science* rather than *advocacy*, as has been recommended by Fuhlendorf et al. (1999).

Third, universities are the rearing grounds for undergraduate and graduate students who will become the next generations of *range management scientists* and *range management technicians*. Lack of students will eventually translate into a smaller quantity and a lower quality of these professionals. The membership of students and other young professionals is essential for a healthy demographic structure of membership in the Society for Range Management. The current demographics of the Society are already skewed in favor of older members. The universities are the source of young professionals, who are the new and typically long-term members of the Society.

Over the past 20 years, the land-grant universities have gradually become less dedicated to the traditionally broad land-grant mission, and have come to operate more like businesses with self interest, providing selective, high value (to the institution) products, in both research and education. Management generally has proven to be less lucrative to these institutions than has intensive, technological science. An arguably shortsighted, specious ethic has developed that we can engineer our way out of problems more effectively than we can manage them, fueled partly no doubt by the historical observation that people have often proven less than proficient at management. At these universities, traditional range management, with its history of poor extramural financial support, and limited student interest, in a phrase, *hasn't cut it*. As a result, range management programs, especially some of the stronger programs, have been scaled back, and range management programs at the major universities, including the land-grant universities, are, in many senses, weaker than they have been in decades.

Given the current and increasing predominance of financial considerations in determining the viability of programs at land-grant universities, the future prospects for traditional range management programs at these institutions do not seem bright. One possibility for contributing some improvement of these prospects is to adopt the inclusive concept of range management described in this paper. Adoption of this approach has several advantages.

First, by becoming a true, integrative management science, range management science can become the program of choice for undergraduate and graduate students with diverse interests in *integrated natural resource management*. In a disciplinary landscape of well-established environmental and production sciences, a strong, identifiable discipline does not currently exist that is directed at broad considerations of active management of human, environmental, and physical resources. Range management science can fill this disciplinary vacuum at the region's land-grant universities, especially in a region of predominantly arid rangeland like the western United States. The students, at least, are there. To offer coherent programs, faculty members at these institutions will, at the most philosophical level, need to find *common* identity within the core of range management science of Figure 5, not only the traditional, comfortable, discrete identities within the mantle.

Second, compared with the narrow disciplinary implications of the pedestrian image of traditional range management, the adoption of *range management science* will provide increased scientific credibility and technical identification at these institutions. The name provides a claim of relevance to both *science* and *management.*

Third, the philosophical breadth of a *range management science* program still allows each institution the philosophical space to design a program to accommodate the regional needs or unique characteristics of its students. The emphases desired within range management science programs by students can be radically different at, for example, the University of Wyoming than at Humboldt State University. Range management science provides situational flexibility while maintaining disciplinary integrity. Also, its philosophical breadth offers the possibility of more potential homes within the administrative units of academic institutions,

Fourth, notwithstanding the current trends favoring bioengineering over management of agricultural and ecological systems, and favoring unmanaged preservation over managed production and managed conservation, the longer-term future trends are unclear. Increasing human population and increasing demands on natural resources will continue to increase interest in *multiple efficiencies*. The inherent integrated diversity of *range management science* should be especially advantageous in the design, development and implementation of management systems to address multiple *efficiencies* rather than traditional, single-product *production.* Those same increasing human demands, and the desire to formulate environmentally friendly solutions to ecological problems such as weed invasions, catastrophic fires, etc., should inevitably favor an increased role for active, integrated management, on lands held for ecological preservation.

Most of the natural resource disciplines arose to control damage from the intensive activities of technical specialists of different kinds; these disciplines arose to clean up the created problems of private or public engineers of one kind or another. Looking ahead, the proliferation of bioengineers and other technical scientists of all kinds, and the sometimes unsystematic, tactical tinkering of their work, when combined with an increasing interest in preserving natural landscapes in the presence of such human engineering, portend plenty of opportunities in the future to design and develop integrated solutions to manmade problems. Range management science, as envisioned in this paper, should be well positioned to address these likely future opportunities with integrative management solutions, whether the current pro-technology trend continues, in the event of a strengthened anti-technology social countertrend, or in the likely case that both trends proceed simultaneously. In any case, the increasingly complex objectives of modern activities, and increasing interest in interdisciplinary, cooperative research promise scholarly and financial opportunities for a *range management science* designed to integrate specialized sciences, address multiple objectives, achieve multiple efficiencies, and communicate accurate, useful information.

The curricula at the universities interested in *range management science* will need to be individually, significantly re-oriented to strengthen skills in, among other areas, systems science, art and design, and communication. In graduate programs, increased attention will need to be directed at interdisciplinary projects. Considerations and pursuit of *art* and *design* of integrative abstractions, more than just multi-disciplinary science, will be needed to elevate graduate projects above case studies, and provide the synthesis to raise studies to the level of management science. Details of other likely changes are beyond the scope of this paper, but the Society for Range Management, through its committees on education and accreditation, can assist in the design of these educational curricula in range management science.

International Dimensions of Range Management Science

Many of the contributions to range management science from outside of North America, including the contributions from development projects in developing countries, have involved more integrated management science than specialized, basic or applied science. In fact, professionals involved in international development projects in developing countries, in their efforts to design creative, adaptive, or coordinated management plans rather than specialized, technical research, have been, in many cases, unequivocal leaders in developing some of the kinds of syntheses that are at the core of range management science. Some of this work has been conducted within development concepts such as *farming systems, agroforestry*, etc. Unfortunately, preoccupation with specialized, experimental science has marginalized many of the synthetic, scientific contributions of many of these scientists and technicians. In some cases, a combination of scholarly elitism and a narrow concept of research have shunted such efforts toward broad-minded but respected technical publications, and away from experimentally-oriented publications, including, to some degree, the *Journal of Range Management.*

The identity and development of range management science have not benefited from this parochialism. No doubt, membership in the Society for Range Management has suffered.

For reasons of both *science* and *business*, the Society for Range Management needs enhanced pursuit of the international dimensions of range management science. An inclusive philosophy of range management science, a Society for Range Management that views diversity synergistically, and a *Journal of Range Management Science* that is broad in concept, significantly, and inherently, increase the potential for international activities in the Society for Range Management.

Recently, M. M. Kothmann (personal communication) related that the Board of Directors of the Society for Range

Management had (again) discussed renaming the Society for Range Management the *International* Society for Range Management. Such action would have significant potential value, insignificant disadvantages, and little cost (at least beyond the expansion of the editorial board of the Journal that was discussed previously). *A Journal of Range Management Science,* with a sub-heading of *A Journal of the International Society for Range Management* would clearly show that the Society is interested in attracting international members, and their scientific contributions.

Concerning the Next Incarnation of the Range Glossary Committee

Developing range management science beyond philosophical generalities will require increased efforts in the area of concept design. Many of our concepts used in range management over the years have been developed for ad hoc applications in management, and are inadequately designed for optimal use in a management science (For an example, see Scarnecchia (2004a). Because concepts of many kinds are the functional tools of a management science, development of an improved management science will require greatly increased efforts in the *synthesis* of concepts. An earlier paper (Scarnecchia 1996) examined some basic considerations, including abstracting and confounding, that are involved in the design of concepts for range management science. That same paper explained the idea of a conceptual hierarchy, from the simplest of a group of related concepts to the most complex.

We have never had a comprehensive examination of the concepts used in range management, and an evaluation of their general utility in range management science. Because definition requires conceptuality (Fuller 1975), and because synthetic concepts of varying complexities are at the core of range management science, the next Range Glossary Committee should consider focusing more on developing a glossary of concepts rather than a glossary of definitions. A glossary of concepts should differ from the past editions of the *Glossary of Terms Used in Range Management* in several ways.

First, significantly more care should be given to citing the sources of the concepts and corresponding definitions used. Such care is more in line with the standard protocol of scientific citation, and rigorous citation also provides important supporting documentation to the concepts. Such documentation would stretch the inherently limited format of a glossary.

Second, the definitions should be annotated with supporting analyses and descriptions. The descriptive and analytical annotations should include such matters as the origin (s) of the concept, some characterization of the concept, the kind of communication function the concept is designed to accomplish in range management science, relevant past applications, and description of at least some of its appropriate applications. Variations within and outside of range management science should be noted. The supporting analyses and evaluations recommended here will require a publication of significantly greater length, detail, and organization than the previous *booklets*.

Third, the design of the entire *book of concepts* should ideally be based on some generalized classification of concepts—possibly a hierarchical classification—one arranged according to the relative complexity or the abstraction or interactivity of each concept within range management science. Achievement of this objective will require a significant effort directed at synthesis and design before and during the development of the book of concepts. The individuals on the committee to undertake this effort should have diverse backgrounds and experiences, but because conceptuality inherently involves abstraction, the individuals should all have interest and skill in abstract thinking.

A book of concepts as described here would be a significant contribution toward establishing a stronger identity for range management science. It would be a logical effort for the Society for Range Management, because the Society would be the principal institutional force with a stake in the establishment and furtherance of range management science.

Empowering Diversity

No theme at the recent Annual Meeting of the Society for Range Management was more forceful and pervasive than *diversity.* The nametags for the meeting read *Rangelands: Diversity through Time.* I heard several speakers refer to this theme in referring to the importance of biodiversity on rangelands. The theme was admirable, but everything I saw at that meeting reminded me that I would have omitted the colon in the title by omitting the first word.

From its earliest conception as a management art, to its many manifestations as *comprehensive management*, to its conception here as *range management science*, the science has, intentionally, unknowingly, or inevitably, sought identity in inclusive, integrative solutions to questions involving diverse elements. The diversity involves more than just biodiversity on rangeland; it involves diversity of contributing sciences, viewpoints, cultures, people, products, processes, values, objectives and efficiencies.

As a philosophical concept, range management science should bring increased diversity of scientists and ideas to the Society for Range Management. In the process, the already ongoing increase in social diversity in the Society will be naturally fostered in an unforced, evolutionary environment. Such unforced social diversity will assist in maintenance of philosophical unity and professional integrity within the Society.

The Future and Range Management Science

The challenges facing the Society for Range Management should be addressed comprehensively. In the absence of significant, substantive changes, current trends are not encouraging. Continued inaction seems risky, and unwise.

We need to be counter-intuitive here, and resist the defensive tendencies to indulge in expedient political or pseudo-scientific advocacy, or to withdraw scientifically to specialized sub-sciences like range ecology or range animal science. Instead, we should pursue a diverse, inclusive, dynamic concept of range management science because it is a sound strategic course—a course that has scientific space, creative opportunity, and professional integrity. While success is not guaranteed, the inclusiveness of this concept of range management science increases the potential for success, and reduces the risk of extinction due to specialization without a definable specialty.

The concept of *range management science* described here is designed to accommodate virtually everyone within the Society for Range Management, and to attract others to the Society. It is more empirically interpretive than radically creative; it conceptualizes and accommodates the naturally evolving trends in range science and in the Society for Range Management's professionals. Designed to interpret what is happening to range science and range management in a complex, natural, competitive environment, *range management science* as a concept owes more to the subtleties of ecological influence than the force of agricultural imposition (Scarnecchia 2003). And precisely because it is not forced, because it is derived by listening to the cultural landscape, it is a low risk proposition.

In a sense, the design of this paper, involving diverse elements, integrative analysis, and multiple objectives, is an example of the kind of synthesis that is at the core of range management science; this paper exemplifies what it espouses. The vision it presents is an harmonious one; it gives range management science a strong, identifiable, marketable identity. That vision involves and promotes precise language, transparent actions, and effective communication. Range management science is designed to take full advantage of the diversity of content that has fragmented range science as a technical science, and the diversity of perspectives that has clouded range management as an applied profession. The concept of *range management science* empowers the diversity of its contributing sciences and of its working professionals, and establishes a philosophical environment of technical and social unity where the scientific, institutional, informational, and professional synergies we need can flourish.

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Recreationist responses to livestock grazing in a new national monument

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Abstract

Several U.S. rangeland areas recently have been designated as national monuments to protect scientifically or culturally important resources. Typically recreation and livestock uses have been retained in these areas. Because some people believe protection and use are incompatible, and because monument designation can increase public scrutiny of management while attracting new visitors to the area, we surveyed hunters and hikers in the Grand Staircase-Escalante National Monument, Utah, about their perceptions of livestock grazing in the monument. We examined associations between visitors' personal characteristics and their reports of how livestock grazing and multiple-use management affect recreation experiences. Recreation activity type was a significant predictor of experience effects, but we found no evidence that the act of designating a national monument itself affected experiences. Locations of current and childhood residence also were significantly associated with experience effects. Because designation tends to attract certain types of visitors more than others, creating rangeland national monuments may foster increased conflict between recreation and livestock grazing uses in those areas.

Resumen

Varias áreas de los pastizales naturales de los Estados Unidos han sido designados recientemente como monumentos nacionales para proteger recursos científicos o culturales importantes. Típicamente los usos para esparcimiento y pastoreo han sido retenidos en estas áreas. Debido a que alguna gente cree que la protección y el uso de los pastizales son incompatibles, y porque la designación de un monumento nacional puede aumentar el escrutinio público del manejo, atrayendo al mismo tiempo nuevos vistantes al área, encuestamos cazadores y excursionistas en el Grand Staircase-Escalante National Monument, Utah, sobre sus opiniones del pastoreo en el monumento. Examinamos la relación entre las características personales de los visitantes y sus informes sobre el efecto del pastoreo y el manejo de uso múltiple sobre sus experiencias recreativas. El tipo de actividad del esparcimiento fue un predictor significativo de las opiniones de la experiencia, pero no encontramos ninguna evidencia que el acto de designación de un monumento nacional sí mismo afectara las percepciones. Las localidades de la residencia actual y de la niñez también fueron asociadas significativamente con las percepciones. Debido a que la designación tiende a atraer ciertos tipos de visitantes más que a otros, la creación de los monumentos nacionales de pastizales puede fomentar conflicto creciente entre los usos para esparcimiento y para pastoreo en esas áreas.

Public rangelands in the U.S. are managed for a wide range of social values, from commodities such as water and forage to less tangible services such as scenery, open space, and biodiversity (Hartmann et al. 1988, McClaran et al. 2001). Some highly vocal segments of society insist that environmental benefits to rare plants and animals, watersheds, and recreation opportunities must be enhanced by eliminating livestock grazing (Ferguson and Ferguson 1983, Wuerthner and Matteson 2002). In response, a political movement to protect traditional range uses, especially grazing, has emerged (Huffman 1994, Raymond 1997). These conflicting views have affected public land policymaking at the highest levels.

In 1996 the Grand Staircase-Escalante National Monument (GSENM) in southern Utah was designated to protect outstanding geology, paleontology, archeology, biology and history. Responding to competing political forces, President Clinton declared that the new monument would be of unprecedented size for the lower 48 states, yet he also took the unusual step of proclaiming livestock grazing as a legitimate use (Clinton 1996). Although the proclamation does not mention recreation uses other than hunting, national monuments typically are managed for outdoor recreation, and parts of the GSENM have been popular recreation settings for many years. The Bureau of Land Management (BLM) retained management authority for the area, making it that agency's first national monument. Since the BLM manages for multiple use as mandated by the Federal Lands Policy and Management Act, GSENM managers needed to strike a balance between use and protection that potentially would differ from the agency's standard practices, but also from visitors' basic assumptions about the character of a national monument.

Before his term ended in January 2001, Clinton declared 14 more BLM national monuments, most of which face the same pressure to balance protective, recreational, and grazing management objectives. To find that balance, rangeland managers need information about the perceptions that recreation visitors have regarding other monument uses and values. It is important to know how different types of visitors respond to the presence of

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This research was supported by the U.S. Department of Interior-Bureau of Land Management; the Institute for Outdoor Recreation and Tourism, Utah State University; and the Utah Agricultural Experiment Station, Logan, Utah 84322. Approved as UAES journal paper No. 7462.

Manuscript accepted 9 Jan. 03.

livestock, and moreover how designation of a national monument affects such responses. By understanding the characteristics of visitors who have antipathy toward grazing, managers are better equipped to address recreation/grazing conflicts. Alternatively, if recreationists report that their experiences are positively or neutrally affected by livestock grazing in some circumstances, managers can try to promote grazing primarily under those circumstances. Accordingly in 1999 we surveyed GSENM visitors about monument values, livestock grazing, and multiple-use management.

Grazing engenders strong feelings among rangeland stakeholders. In the literature of political advocacy, cows are often blamed for ecological and social problems on public lands. Opponents of public lands grazing say that cattle pollute scarce desert water sources, spread exotic plant species, expose soils to erosion, compete with wildlife for food, and damage archaeological and paleontological sites (Hedden 1999, Wuerthner and Matteson 2002). Involvement in outdoor recreation tends to be positively associated with measures of environmental concern (Dunlap and Heffernan 1975, Theodori et al. 1998), so we might expect an increase in recreation use caused by designation of the GSENM to lead to an increase in complaints about livestock use and impacts.

Studies of the link between outdoor recreation participation and environmental attitudes have not focused specifically on grazing, but there is limited evidence that perceptions of livestock use are associated with recreation activity style, classification of the land where grazing occurs, general environmental beliefs, and demographic characteristics. Sanderson et al. (1986) examined how national forest recreationists in Oregon reacted to grazing management practices. They measured ratings of scenic beauty in photographs that illustrated different levels of grazing management, and found these were significantly related to recreation activity. Fishermen rated most photographs less attractive than did hunters or campers, and seemed most sensitive to the relationship between livestock grazing and riparian areas; hunters rated photographs consistently higher than other groups. Breadth in recreation participation is positively related to support for grazing management (Sanderson et al. 1986, Brunson and Rasmussen 1995), i.e., the more variety there is in people's rangeland recreation repertoires, the less likely they are to judge grazing practices negatively. In particular, studies show that consumptive recreationists such as hunters differ from non-consumptive users in some, though not all, aspects of environmental attitudes (Dunlap and Heffernan 1975, Donnelly and Vaske 1995, Theodori et al. 1998). Therefore we hypothesized that hikers and hunters would differ significantly in their perceptions of cattle grazing in the monument.

The location of encounters with grazing also affects visitor perception. Sanderson et al. (1986) found that frequent visitors to an area were more likely to accept intensive grazing management, but they also found that people who experienced close contact with cattle were more likely to express negative perceptions. Mitchell et al. (1996) found that visitors in dispersed campsites tended to be more critical of grazing than those in developed campgrounds, which are usually fenced off from livestock use. While there is little research to show that the act of land-use reclassification affects environmental perception, there is widespread popular belief in such a "designation effect" (Nash 1982, Power 1997). Land designations carry implications about the extent of influence on human activities: Hodgson and Thayer (1979) and Anderson (1981) found that lands with a protective designation (e.g., national park, wilderness) are evaluated differently than those with multiple-use designations. Johnson et al. (1997) found that respondents were more tolerant of grazing on non-wilderness public lands than on wilderness lands. These findings suggest that national monument designation could create a more idealized view of an area, especially among those who did not know it before designation. Those who had visited previously would be more likely to expect cattle (even though they might assume designation included a ban on grazing) and thus to tolerate their presence. Therefore, we hypothesized the pre- and post-designation users would differ significantly in their perceptions of grazing.

Research has shown that some sociodemographic characteristics are associated with judgments about nature and its management, including perceptions of grazing management. General environmental orientations have been found to vary with such personal attributes as age (Pierce et al. 1992), gender (Mohai 1992), education (Steel et al. 1990), rural/urban residence (Howell and Laska 1992), and economic dependence on natural resources (Brunson et al. 1997).

In a survey about federal rangelands and their management, Brunson and Steel (1996) found support for an urban/rural dichotomy in attitudes and beliefs, especially if the rural economy depends on rangelands. They also found that attitudes toward range management were driven by overall environmental attitudes. Sanderson et al. (1986) found that attitudes about range management varied by place of residence. Mitchell et al. (1996) found that the geographic location of a respondent's hometown was associated with perceptions of grazing, but the size of the community was not. We hypothesized that there would be significant associations between grazing perceptions and sociodemographic characteristics.

Materials and Methods

Study area

Sheep and cattle grazing has occurred in the Grand Staircase-Escalante region since Mormon pioneers settled the area in the spring of 1875, drawn by the mild climate and relative abundance of grazing land (Powell 1994). The small towns of Escalante and Boulder remained frontier outposts for many years. Isolated from major highways and large cities, their growth was limited by what the natural resources could sustain. As access and facilities for travelers slowly improved, the area's sandstone canyons attracted increasing numbers of tourists to hike the Escalante River, view ancient indigenous rock art and structures, follow the historic Hole-in-the-Rock Trail, or drive scenic highways connecting the region with other national parks and monuments. The local economy today depends on tourism as much as on the natural resource mainstays of livestock and timber (Farmer 1999).

Designation of the area's public lands as a federally protected national monument afforded the area certain environmental protections as indicated under the Antiquities Act of 1906 and the presidential proclamation (Clinton 1996). Mining projects were shelved and limits were placed on some extractive uses. Despite these changes, federally leased grazing allotments were not immediately affected by the act of designation.

Measures

Our measurement instruments were surveys administered by mail. We designed separate questionnaires for hunters and backcountry visitors, but most survey items were identical and thus the responses can be compared. Surveys addressed several issues of interest to Grand Staircase-Escalante National Monument

(GSENM) managers, including grazing perceptions. Specific variables used in the analysis described here include: frequency of sightings of cattle or evidence of cattle; qualitative evaluations of the vegetation condition and protected features; evaluations of whether livestock grazing or multiple-use management added to or detracted from recreation experiences; and personal characteristics of visitors.

Pre- and post-designation users were determined by means of a question asking when a respondent had first visited the monument. Visitors reporting 1996 or earlier were classified as "pre-designation." Visitation is highest in spring, and designation occurred in September 1996. Thus it is possible that respondents whose first visit was in 1996 already knew about designation, but that number is very small. Visitors who reported making their first visit in 1997 or later were classified as "post-designation." For this portion of the analysis only hikers were compared since the primary destination for hunters is not the monument but a particular hunting area.

Sampling

Hunters were contacted through a Fall 1999 hunter registration list maintained by the Utah Division of Wildlife Resources for its Paunsaugunt hunting unit, which is famous for its trophy mule deer hunting. Because only part of that unit falls within the GSENM, hunters were asked to fill out the survey only if they had hunted or scouted inside the monument. A map was provided to help hunters determine whether they had done so. Those who had hunted or scouted within the monument were asked to complete and return the survey; those who had not were asked to check a box on the cover and return the survey uncompleted.

No equivalent registration list exists for hikers. Backcountry hikers in a large, remote area such as the GSENM constitute a somewhat rare and elusive study population; to obtain the broadest possible sample, in March–September 1999 we assembled a list of visitor names and addresses from 3 sources: direct contacts by a researcher during GSENM visits, postcards placed on windshields of vehicles parked at trailheads, and participants in a voluntary backcountry permit system administered by the BLM.

On-site contacts occurred on trails and at trailheads. Although sampling times and sites covered the full range of hiking opportunities, we over-sampled on weekends and holidays, and at popular trails, to increase the chance of obtaining a statistically viable sample. Researchers approached all recreationists encountered during contact periods; if the visitor was engaged in backcountry hiking (i.e., non-motorized foot travel that entailed going one or more miles from one's vehicle), he or she was asked to participate in the survey and to supply a name and address for a subsequent mail questionnaire. When an unattended vehicle was seen at a trailhead, a postcard was placed on the windshield. The cards briefly described the survey and asked visitors to supply a name and address and return the card if their trip fit the criteria for backcountry use. All persons who returned a postcard received a questionnaire by mail.

Bureau of Land Management (BLM) employees supplied a list of addresses of persons who filled out voluntary permit forms available at the GSENM visitor center in Escalante and at many backcountry trailheads. Addresses of persons who already had been contacted in person were eliminated from this sample, and the remainder received mail questionnaires. Cover letters for this group differed slightly from those for the other 2 samples since the recipients had no previous knowledge that they would be receiving a survey, but the questionnaires themselves were identical.

Before combining hiker samples obtained in these different ways, it was necessary to compare responses across groups. Chi-square tests for comparison of frequency distributions were conducted for visitor attributes used in this analysis (sex, childhood residence, current state of residence, education), as well as the reported frequency of encounters with cattle or evidence of livestock use. No comparisons found statistically significant differences (α=.05), suggesting that all 3 sampling methods obtained members of the same population of backcountry hikers.

As a census of permit-holders, the hunter sample can be considered representative of the population of GSENM hunters. However, we cannot be as certain that the hiker sample was representative of the entire population of backcountry hikers in the GSENM. Because we over-sampled on days when visitor numbers were likely to be highest, persons who deliberately seek to avoid other visitors may be under-represented. Similarly, persons who prefer to minimize contact with managers might have been less likely to return windshield postcards or participate in a voluntary registration system. Previous research has shown that certain types of visitors may be less likely than others to use unattended trail registers; e.g., Lucas and Oltman (1971) found in a study of Oregon wilderness hikers that persons hiking alone, women, and people making comparatively shorter visits were less likely to sign trailhead registers.

Nonetheless, we are confident that we contacted the broadest possible cross-section of the GSENM hiker population given the constraints of the sampling situation, i.e., a relatively sparse, irregularly distributed population within a large (>9,000 km^2) area. Moreover our response rates were very high for a lengthy, complex mail survey. Of 327 hikers who were contacted in person or by postcard, 277 completed and returned their surveys while 4 surveys were undeliverable, yielding a response rate of 86%. For the 396 hikers sampled by voluntary permits, 32 surveys were undeliverable and 275 (76% of deliverable surveys) were completed and returned. Hunter surveys were mailed to 327 people; 5 surveys were undeliverable and 216 (67%) were either completed or returned by persons who did not hunt or scout in the GSENM. Because response rates were high, we did not attempt to contact non-respondents.

Analysis

Chi-square tests for differences in frequency distribution were used to assess whether perceptions of livestock grazing in the monument were associated with socio-demographic characteristics, recreation activity, or timing of first visit.

Due to inter-correlation among variables (e.g., hunters were overwhelmingly male, older people were more likely to have grown up in rural areas), polychotomous logistic regression estimates were obtained in order to isolate the associations between particular visitor characteristics and perceived impacts of management activities on recreation experiences. Polychotomous (or multinomial) logistic regression is a procedure that can be used to estimate the influence of non-continuous predictor variables on a categorical dependent variable (Bohrnstedt and Knoke 1994). This procedure produces separate logistic regression equations that predict p_{ij}, (i.e., the probability that the ith case is in the jth category of the dependent variable). N-1 models are obtained in this manner, where N is the number of baseline categories. In this analysis the dependent variables – influence of livestock grazing and awareness of multiple-use on recreation experiences—contained 3 categories: "detracts from experience," "neutral," or "adds to experience." The latter was the omitted baseline category. With the exception of age, all characteristics were operationalized as dichotomous dummy variables; age was collapsed into 4 categories (under 25, 25–40, 41–55, over 55).

Table 1. Frequency of sightings by hunters and hikers of cattle or evidence of cattle in the Grand Staircase-Escalante National Monument (GSENM), 1999.

Impact type Recreation group	Never	Rarely	Occasionally	Frequently	Chi-square(p)[1]
	----------	----------	(%)	----------	
Cattle seen					
Hunters (N = 155)	1	7	28	64	73.2 (<.001)
Hikers (N = 522)	22	19	28	31	
Evidence seen					
Hunters	1	7	26	66	10.7 (.014)
Hikers	7	11	27	55	

[1] The chi-square statistic here indicates probability that differences in frequency distributions of answers between hunters and hikers are attributable to random error.

Table 2. Reported effect of seeing cattle or knowing the area is open to multiple-use management on the quality of recreation experiences in the GSENM, 1999.

Impact Type Recreation Group	Detracts from Experience	Neutral	Adds to Experience	Chi-square (p)
	----------	(%)	----------	
Seeing cattle[1]				
Hunters	39.1	35.8	25.2	56.3 (<.001)
Hikers	70.0	22.3	7.8	
Multiple-use[2]				
Hunters	2.6	14.6	82.8	97.8 (<.001)
Hikers	33.6	28.0	38.4	

Results

Hunters and Hikers

Hunters made up 22% of the total sample (N = 155) and hikers 78% (N = 552). Hunters were more likely than hikers to report having seen cattle or evidence of cattle (Table 1), though both groups reported seeing evidence of cattle frequently. Probably this is due to the locations where their activities take place. Most hikers visit the Escalante Canyons area where a number of grazing allotments have been retired since 1996, while hunting typically occurs in the western third of the monument where grazing is still the rule. When asked to attribute a cause for any vegetation impacts they encountered, both groups tended to mention cattle, but the tendency was greater among hunters than hikers (70% vs. 44%). Hikers were more likely to ascribe impacts to human uses (33% vs. 7%) (χ^2=41.9, p=.013).

Respondents were asked if seeing cattle, or knowing that the area is open to multiple-use management, affected the quality of their recreation experiences (Table 2). Hunters were significantly less likely to report that seeing cattle detracted from their recreation experiences, and more likely to report that seeing cattle enhanced the experience. Similarly hunters were less likely to say that knowing the area is open to multiple-use management detracted from experiences and much more likely to say that it added to their experiences.

Pre-Designation and Post-Designation Users

Of 552 hiker respondents, 49% were classified as pre-designation visitors and 49% as post-designation; dates of first visits were missing for the remaining respondents. Comparisons between pre- and post-designation visitors found no significant differences in frequency of cattle sightings, frequency of sighting evidence of cattle, judgments of vegetation impacts, judgments of impacts to other monument features, or the extent to which cattle grazing and multiple-use management influenced their recreation experiences positively or negatively.

Demographic Characteristics

Respondents were predominantly male (72% of hikers, 91% of hunters), with an average age of 37 in both groups. Hunters were more likely than hikers to live in Utah (87% vs. 33%) and to have grown up in a small town or rural area instead of a city or suburb (68% vs. 30%). Median education levels were: high school diploma for hunters; Bachelor's degree for hikers.

Table 3 summarizes the relationships between 5 demographic characteristics and respondents' perceptions of the impact that livestock grazing and multiple-use management had on their monument recreation experiences. Each of the relationships listed was identified by means of a chi-square test for differences in frequency distribution (α = .05). We found no association between gender and influences of grazing and multiple-use management. Age was not associated with a perception of multiple-use management overall but was associated with perceptions of livestock grazing, as visitors age 65 and older were half as likely as younger visitors to say that seeing cattle strongly detracted from their visit. Utah residents, persons who grew up in a small town or rural area, and persons with lower levels of educational attainment were less likely to say that seeing livestock grazing or

Table 3. Summary of relationships between demographic characteristics and influences of livestock grazing and multiple use management on recreation experiences, GSENM, 1999.

Potential influence	Utah resident?	Age	Gender	Residence	Childhood Education
Livestock Grazing	Utahns less likely to say "detracted"*	Older residents less likely to say "detracted"	NS	Rural residents less likely to say "detracted"	Less-educated less likely to say "detracted"
Multiple-use Activities	Utahns less likely to say "detracted	NS	NS	Rural residents less likely to say "detracted"	Less-educated less likely to say "detracted"

*χ^2 test for difference in frequency distribution, P < .05

Table 4. Parameter estimates for polychotomous logistic regression of the reported effect upon recreation experiences of seeing livestock grazing (omitted category: persons for whom grazing added to the experience), GSENM, 1999.

Variable	Logistic Coefficient	Standard Error	T ratio
Detracted from experience (N = 395):			
Constant	.51	.42	1.22
State (1 = Utah, 0 = other)	.69	.34	2.04*
Sex (1 = Male, 0 = female)	-.63	.33	–1.88
Pre/post designation (1 = pre, 0 = post)	-.08	.30	–0.26
Childhood locale (1 = rural, 0 = urban)	.84	.30	3.17**
Education (1 = college, 0 = high school)	-.15	.33	–0.45
Activity type (1 = hiker, 0 = hunter)	–1.23	.37	–3.35**
Age under 25	.81	.50	1.63
Age 26-40	1.15	.38	3.05**
Age 41-55	1.57	.39	4.01**
Did not affect experience (N = 162)			
Intercept	-.20	.46	–0.44
State (1 = Utah, 0 = other)	.43	.36	1.20
Sex (1 = Male, 0 = female)	–.57	.36	–1.61
Pre/post designation (1 = pre, 0 = post)	.30	.31	0.95
Childhood locale (1 = rural, 0 = urban)	.52	.31	1.65
Education (1 = college, 0 = high school)	15	.35	0.33
Activity type (1 = hiker, 0 = hunter)	–.48	.39	–1.18
Age under 25	.48	.45	0.90
Age 26–40	.75	.40	1.86
Age 41–55	1.28	.42	3.09*

*P < .05 **P < .01

knowing the area is open to multiple-use activities detracted from their visits to the monument.

Before concluding that perceptions are associated with demographic characteristics, we considered an alternate hypothesis that the differences in recreation experience perceptions were a function of differences in the extent to which persons in various demographic categories encountered evidence of grazing and multiple-use. Therefore we measured correlations between reported encounters and demographic characteristics. We found only 1 such correlation: older visitors were slightly less likely to report seeing evidence of livestock (perhaps because they travel fewer miles on foot). Therefore we interpret the findings as evidence that acceptability of grazing and multiple-use management is associated with demographic factors.

All Visitor Characteristics

Analysis of the relationship between demographic characteristics and the effect of livestock grazing on recreation experience (Table 4) shows that the effect of livestock grazing on recreation experience is dependent upon current state of residence, rural/urban nature of one's childhood residence, type of recreation activity, and age. Visitors are more likely to say grazing detracted from the experience if they are from outside Utah, grew up in an urban area, hiked, or are between the ages of 26 and 55. The only variable that influences whether grazing had no effect is age: 41- to 55-year olds are more likely than other age groups to say there was no effect, and less likely to say grazing added to the experience.

Analysis of the relationship between demographic characteristics and the effect of knowing the area is open to multiple-use activities on recreation experience (Table 5) shows that experience perceptions are associated with state of current residence, location of childhood residence, education, and activity type. Visitors are more likely to say their experience was negatively affected by knowing the area is open to multiple-use if they are from out of state, grew up in an urban area, graduated from college, or hiked. They were more likely to say there was no effect (rather than to say it added to the experience) if they were from out-of-state, grew up in an urban area, or hiked.

Discussion

We hypothesized that there would be significant differences between hunter and hiker perceptions of livestock grazing. This hypothesis was supported. Hunters saw cattle and evidence of cattle more often than hikers, partly because hiking tends to take place in areas where less livestock grazing takes place, and perhaps also because hunters venture off trails and away from canyons more than hikers. They were less likely to say that livestock grazing detracted from their experiences; however, those hunters who reported moderate or heavy vegetation impacts were more likely than hikers to attribute those impacts to cattle. It may seem counterintu-

Table 5. Parameter estimates for polychotomous logistic regression of the reported effect upon recreation experiences of knowing the area is open to multiple use (omitted category: persons for whom knowing about multiple-use added to the experience), GSENM, 1999.

Variable	Logistic Coefficient	Standard Error	T ratio
Detracted from experience (N = 173):			
Intercept	–.84	.37	–2.28*
State (1 = Utah, 0 = other)	.77	.25	3.14*
Sex (1 = Male, 0 = female)	–.27	.25	–1.09
Pre/post designation (1 = pre, 0 = post)	–.37	.23	–1.61
Childhood locale (1 = rural, 0 = urban)	.5	.23	2.45*
Education (1 = college, 0 = high school)	–.90	.30	–2.95**
Activity type (1 = hiker, 0 = hunter)	–2.44	.54	–4.45**
Age under 25	.67	.45	1.48
Age 26–40	.54	.33	1.63
Age 41–55	.01	.32	0.15
No effect on experience: (N = 164)			
Intercept	–1.15	.37	–3.15**
State (1 = Utah, 0 = other)	.53	.24	2.21*
Sex (1 = Male, 0 = female)	.00	.24	0.01
Pre/post designation (1 = pre, 0 = post)	–.01	.22	–0.05
Childhood locale (1 = rural, 0 = urban)	.50	.22	2.27*
Education (1 = college, 0 = high school)	–.41	.25	–1.64
Activity type (1 = hiker, 0 = hunter)	–.66	.30	–2.17*
Age under 25	.54	.43	1.30
Age 26–40	.39	.33	1.18
Age 41–55	.25	.31	0.80

*P <. 05 **P <. 01

itive that hunters were more likely to attribute impacts to cattle while less likely to mind seeing them, but this may be a reflection of demographics: Hunters were more likely to have a rural childhood and to be from Utah, and therefore may be more used to seeing and identifying impacts, but also more tolerant of cattle and their effects on vegetation. More than half of all hunters said knowing the area is open to multiple uses "strongly added" to their experiences. To some extent this is probably a political statement: Since national monuments have usually been managed as protected areas where hunting is not an allowed use, hunters may simply be indicating that multiple-use management means they are less likely to be barred from their preferred activity within the GSENM.

Based on the findings of Hodgson and Thayer (1979) and Anderson (1981), who found that protective designations affect how people think about natural places, we also hypothesized that there would be significant differences in perceptions of persons who had visited the area prior to designation versus those who knew it only as a national monument. This hypothesis was not supported. Opponents of protected-area designation sometimes argue that such designations make it harder to achieve management objectives even if management options remain ostensibly flexible (e.g., Heidemann 2001). And since growth in protected-area tourism often brings an increase in undesirable environmental impacts (Wang and Miko 1997), it is sometimes argued that protection is actually counter-productive. In this study we were not able to measure changes in conditions as a result of designation, but we were able to compare perceptions of hikers whose ideas about the GSENM were likely to have been formed prior to designation with perceptions of those whose ideas were likely to have been formed subsequent to designation. We found no differences between these 2 groups. This may indicate that the concern about a "designation effect" is overemphasized, or it may simply reflect a situation where pre-designation users were already unhappy about grazing and interactions with livestock.

Finally, we hypothesized that demographic characteristics would be significant predictors of grazing perceptions. This hypothesis was partially supported. Even after controlling for activity, respondents' current and childhood residences and age were associated with negative perceptions of grazing livestock. Education and current and childhood residence were associated with perceptions of multiple-use management irrespective of activity. However, education and age effects were not as strongly associated as other characteristics, and gender was not found to be a predictor of perceptions of either grazing or multiple-use management.

Conclusion and Implications

The question raised at the start of this paper was: Will the designation of rangeland national monuments restrict managers' ability to use livestock grazing and other multiple-use management strategies, even if such management remains legal under terms of the national monument proclamation. Based on this study, we have to answer "yes and no." We did not find evidence that the mere fact of designation affects the perception visitors have regarding a rangeland protected area. However, we did find differences between visitors seeking different types of recreation experiences, as well as differences rooted in the demographic characteristics of visitors. And it's likely that designation will attract more of the types of visitors who are least likely to support traditional range management activities.

Hikers were more likely than hunters in our study to feel negatively toward livestock and multiple-use management. Designation of the Grand Staircase-Escalante National Monument (GSENM) did attract new visitors – nearly twice as many in 1997 as in 1996 (Stauffer 1999). While highway tourists made up the majority of the new visitors, hiking has also increased. Meanwhile, growth in hunting is restricted because of limited-access management intended to maintain a trophy mule-deer hunting experience. Even if hunter access to other rangeland national monuments is not restricted, hiking growth is likely to be greater simply because many more people hike than hunt in the U.S. (Hartmann et al. 1988).

Moreover, designation appears to have brought visitors to the monument from greater distances. Comparing our survey results with those of a study in 1996 just prior to designation (Ruehrwein 1998), we found that hikers in 1999 were younger, and twice as likely to be from a state other than Utah. Since older visitors and Utah residents were significantly less likely to view livestock grazing negatively, designation appears to have increased the likelihood that visitors will be affected negatively by grazing use. Although our sample was not large enough to measure variation in responses by residents of different states, prior studies (e.g., Brunson and Steel 1996, Reiter et al 1999) have shown that persons from outside the Intermountain West feel more negatively toward traditional approaches to range management. If designation of a national monument draws more visitors from outside the immediate region of the monument – as appears to be the case with the GSENM – then one consequence is likely to be an increase in levels of conflict between recreation uses and livestock grazing. As managers of the new BLM monuments finish developing management plans, they would be well advised to develop strategies – e.g., retiring allotments or adjusting grazing seasons in areas of the monument that receive the heaviest visitor use – that can mitigate such conflicts as they arise.

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J. Range Manage.
56: 577–584 November 2003

An evaluation of the federal grazing fee formula

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Abstract

The federal grazing fee is currently set using the Public Rangeland Improvement Act (PRIA) fee formula established in 1978 and modified in 1986. The formula is adjusted annually using indices of private land grazing lease rates (Forage Value Index, FVI), prices received for beef cattle (Beef Cattle Price Index, BCPI), and costs of beef production (Prices Paid Index, PPI). The FVI tracks price movement in the private forage market and was the only index originally proposed to be included in the fee formula. Public land ranchers and the Interdepartmental Grazing Fee Technical Committee assigned to study grazing fee alternatives in the 1960s questioned the ability of the FVI to account for short-term demand, supply, and price equilibrium, and, for this reason, the BCPI and PPI were added to the fee formula. Nearly 40 years of data are now available to evaluate whether adding the BCPI and PPI did, in fact, help explain short-term market fluctuations. Analysis shows that if tracking the private forage market is the primary objective, the fee formula should have included only the FVI. Including the BCPI and the PPI has caused calculated grazing fees to fall further and further behind private land lease rates. Had the $1.23 base fee in the PRIA formula been indexed by only the FVI, the federal grazing fee would have been $4.36 AUM^{-1} instead of $1.43 AUM^{-1} in 2002. It is time to consider the feasibility of a competitive bid system for public lands, or, at the very least, drop the BCPI and PPI indices and adopt a new fee formula that generates more equitable grazing fees.

Key Words: grazing leases, forage value, public lands, public land grazing, grazing permits, Public Rangeland Improvement Act (PRIA)

Resumen

El pago de pastoreo federal es actualmente determinado usando la fórmula de pago del Acta de Mejoramiento de Pastizales Públicos (AMPP) establecida en 1978 y modificada en 1986. La fórmula es ajustada anualmente usando índices de tasas de arrendamiento de pastizales privados (Índice de Valor Forrajero, IVF), precios recibidos para ganado de carne (Índice de Precios de Ganado de Carne, IPGC), y costos de producción de la carne (Índice de Precios Pagados, IPP). El IVF monitorea el movimiento de precio del forraje en el mercado privado y fue el único índice originalmente propuesto para ser incluido en la fórmula de pago. Rancheros de tierras públicas y un Comité Técnico de Pago de Pastoreo asignado para estudiar alternativas en el pago de pastoreo en los 1960s, cuestionaron la habilidad del IVF para contabilizar por la demanda de corto plazo, oferta, y equilibrio del precio, y por esta razón el IPGC y el IPP fueron agregados a la fórmula de pago. Cerca de 30 años de datos están ahora disponibles para evaluar si el agregar el IPGC y el IPP en efecto ayudó a explicar las fluctuaciones del mercado en el corto plazo. Análisis muestran que si monitorear el mercado privado de forraje es el objetivo primario, entonces la fórmula de pago debería haber incluido solamente el IVF. La inclusión del IPGC, y especialmente del IPP, ha causado que los precios de pastoreo calculado caigan cada vez más por debajo de las tasas de arrendamiento de tierras privadas. Si el pago base de $1.23 dólares en la fórmula de la AMPP fuera indexado solamente por el IVF, el pago de pastoreo federal hubiera sido $4.36 UAM^{-1}, en vez de $1.43 UAM^{-1} en el 2002. Es tiempo de considerar la factibilidad de un sistema competitivo de licitamiento para tierras federales, o al menos adoptar una nueva fórmula de pago que genere pagos de pastoreo más equitativos, y destilar los índices de IPGC y IPP.

A long and interesting history of conflict preceded implementation of the current federal grazing fee formula (USDI/USDA 1977, USDA/USDI 1986, 1992). Some of the major areas of contention included the amount charged, how grazing fees were to be adjusted through time, and whether fees should vary in different areas of the West. All of these issues were part of the debate when the Public Rangeland Improvement Act (PRIA) fee formula was adopted in the late 1970s, and the debate continues.

A detailed historical review of grazing fee policy is provided by Backiel and Rogge (1985), while Dutton (1953) concentrated on grazing fee issues within the structure and history of the Forest Service. Table 1 briefly reviews what we feel are the key policy decisions and legislation surrounding the grazing fee issue. This historical progression covers the time from the inception of the Forest Service in 1906 through the passage of PRIA in 1978 and subsequent formula modifications after a 1986 Executive Order (EO) was signed by President Reagan. The political negotiation, debate, and legislation, as detailed, resulted in the PRIA fee formula that is used to set grazing fees on Bureau of Land Management (BLM) and Forest Service (FS) lands today. Recognizing this history is important for assessing whether PRIA has met the objectives of Congress and others that proposed and adopted the fee formula.

In this paper, we review the relevant history and legislation associated with the PRIA fee formula. We discuss the original fee

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Manuscript accepted 15 Feb. 03.

Table 1. An abbreviated history of grazing fees and the PRIA fee formula.

Grazing Fee Study and Legislation	Description
1906 Forest Service Fees Implemented	Forest Service fees were imposed on ranchers and settlers accustomed to free and unrestricted grazing use. Average fees were about \$0.05 AUM^{-1} (Dutton 1953, USDI/USDA 1977, p. 2–4).
1916 Comparable Forest Service Lease Rate Study	In 1916 the U.S. Forest Service attempted to determine fair compensation for national-forest range by studying the rental value of 900 tracts of private land similar to U.S. Forest Service ranges (Dutton 1953).
1924 Rachford Appraisal	Based largely on an appraisal of supposedly comparable privately owned land (Rachford 1924) and the recommendation of Dan Casement, a Kansas livestock producer assigned by the Secretary of Agriculture to review the appraisal, variable fees and the practice of basing fees on the price of beef and lamb was adopted and prevailed in the FS from 1928 until the mid-1960s (Backiel and Rogge 1985, USDI/USDA 1977, p. 2–2). After passage of the Taylor Grazing Act in 1934, the Grazing Service began charging a \$0.05 AUM^{-1} fee on BLM land in 1936. This fee had no specific economic rationale except to cover administrative costs of the land agencies and was a politically negotiated compromise (USDI/USDA 1977, p. 2–3).
1966 Grazing Cost Study	In 1959–1960, an Interdepartmental Task Force was formed to undertake a joint grazing fee study that would be used to develop a uniform approach to grazing fees between the federal land agencies. One of the major responsibilities of the task force was the 1966 Western Livestock Grazing Survey that provided a total grazing cost comparison of nearly 10,000 public land permittees and private land forage lessors. This total cost comparison indicated that, if interest on the permit investment was excluded (which was controversial), a weighted average base grazing fee of \$1.23 AUM^{-1} would make total grazing costs on public and private lands equal. This base rate was a weighted average for both BLM and FS lands, and for cattle and sheep operations (USDI/USDA 1977, p. 2–22). Because total grazing costs were as variable within ranching areas of the West as they were between areas, no statistical basis could be found for differentiating fees between grazing districts or areas (Arthur D. Little 1967, 1968).The weighted average \$1.23 AUM^{-1} cost differential became the base value used in PRIA. Further, the task force proposed to adjust the base fee annually by an index of private grazing land lease rates, the Forage Value Index, or FVI (Backiel and Rogge 1985).
1969 Grazing Fee Proposal	In 1969, a new fee schedule for FS and BLM lands was announced that adapted the proposed fee increases to the \$1.23 AUM^{-1} base rate (USDI/USDA 1977, p. 2–27). The 1969 fee schedule and formula would use the FVI to adjust fees through time. Implementation of the 1969 fee schedule proceeded with controversy and various legal delays and fee moratoriums.
1973 American National Cattlemen's Association proposal	In October 1973, the American National Cattlemen's Association (now the National Cattlemen's Beef Association, NCBA) proposed a new fee formula to the Secretaries of Interior and Agriculture that would use indices of beef prices and prices paid to adjust grazing fees. The 1964–1968 period would serve as the base period for both indices, and, as noted by Backiel and Rogge (1985), the new formula would have shifted the basis for fee adjustment from a private land lease rate equivalency, based on the FVI, to an ability-to-pay basis using the Beef Cattle Price Index (BCPI) and Prices Paid Index (PPI). The new formula was not accepted by the land agencies.
1976 Federal Land Policy and Management Act	The 1976 Federal Land Policy and Management Act (FLPMA) set out major, overall public land management and policy objectives and mandated that a grazing fee study be submitted to Congress within one year. The resulting 1977 Grazing Fee Study evaluated seven alternative procedures for determining grazing fees, including the fee formula proposed by the NCBA and another formula, which eventually became PRIA, proposed by a Technical Committee assigned to review public land grazing fees by the Senate Interior and Insular Affairs committees (USDI/USDA 1977). The technical committee fee formula was supported by livestock interests because, similar to their own proposal, it included livestock prices and production costs as adjustment factors. Inclusion of these price and cost factors was of primary concern to livestock interests and they maintained that severe hardships to thousands of individual ranchers could be avoided by including these indices in the fee formula (Backiel and Rogge 1985, p. 28). The Grazing Fee Technical Committee argued that the FVI would adequately measure the long-term trend grazing fee and forage values. However, they questioned the ability of the index to capture short-term instabilities that result during periods of disequilibrium (USDI/USDA 1977, p. 3–34). They suggested that, by adding the BCPI and PPI, the fee formula would be better able to account for short-term fluctuations in forage demand and supply. It also provided a compromise between the land agencies that wanted to use only the FVI and public land ranchers who wanted to use only the BCPI and PPI. Including all three indices was criticized because beef prices and production costs should already be included when ranchers formulate lease bids based on livestock production value. Research has since shown this to be the case (Van Tassell and McNeley 1997, McCarl and Brokken 1985).

Grazing Fee Study and Legislation	Description
1978 Public Rangeland Improvement Act	House Report 10587, which eventually became PRIA, was introduced in January 1978 and fees were set using the new PRIA fee formula in 1979. Using the PRIA formula, grazing fees increased in both 1979 and 1980. In both years, the 25-percent limit of change that was included in the legislation kept fees below the calculated value. The \$2.36 AUM^{-1} fee in 1980 was the highest fee ever reached, and PRIA-generated fees have trended downwards ever since. The PRIA fee formula is calculated as $\text{Fee}_t = \$1.23 \times \frac{(\text{FVI}_{t-1} + \text{BCPI}_{t-1} - \text{PPI}_{t-1})}{100}$ The data used to estimate the indices are described in detail in USDI/USDA (1977) and USDA/USDI (1992). Kearl (1989) provides a critical review of the data collection procedures and the index components. Historical values for the indices are provided in Appendix A.
1986 Executive Order 12548	The PRIA fee formula expired on December 31, 1985, but was indefinitely extended by Executive Order 12548 (2/14/86) with an imposed minimum fee of \$1.35 AUM^{-1}. The Executive Order also included a provision that changed the data series used to compute the FVI from a \$ AUM^{-1} to a \$ head^{-1} basis. We understand that this change occurred not because of a perceived need for a different data series, but rather the loose language used in the Executive Order, i.e. those writing the order did not recognize that \$ head^{-1} and \$ AUM^{-1} values are not the same and specified \$ head^{-1} instead of the \$ AUM^{-1} index that had historically been used (Personal communication, Mr. Don Waite, former BLM economist, Washington, D.C.). The changes proposed in the Executive Order were implemented with the 1986 fee year.

proposal supported by the BLM and FS that precluded the Beef Cattle Price Index (BCPI) and Prices Paid Index (PPI), and then evaluate whether the addition of these 2 "ability-to-pay" indices help track and explain the movement of grazing lease rates over time, as was originally projected. Similar studies conducted 15 years ago also evaluated the validity of including the ability-to-pay indices in the PRIA fee formula (Brokken and McCarl 1987, McCarl and Brokken 1985). This study provides an update of the analysis and demonstrates the continued problems that adding these indices to the fee formula have created. Finally, we review the policy implications and alternatives available for setting grazing fees on public lands in the future.

Methods

Nearly 40 years of data are available to evaluate whether adding the Beef Cattle Price Index (BCPI) and Prices Paid Index (PPI) to the PRIA fee formula improved the formula's predictive ability as envisioned by a 1977 Grazing Fee Technical Committee. However, changes in data collection and policies have altered how PRIA-generated fees are computed. The data used to compute the Forage Value Index (FVI) was redefined with a 1986 Executive Order (EO) issued by President Ronald Reagan (Table 1). The Executive Order further directed that a minimum fee of \$1.35 AUM^{-1} would be charged under the PRIA fee formula. Only the first change, the redefinition of the FVI index from a \$ AUM^{-1} to \$ head^{-1} was considered in this analysis. The analysis considers grazing fees that would be generated by the unrestricted Public Rangeland Improvement Act (PRIA) formula, ignoring the grazing fee floor set by EO 12548. Additional regressions were done to determine whether results were different when the FVI was calculated on an AUM basis (FVIAUM in Appendix A), as originally structured.

The analysis is conducted with recognition that the data used to compute PRIA indices has been criticized on numerous accounts. Major criticisms include: a relatively small amount of data is collected to represent all of the western states; the FVI is based on hearsay as people are asked to recall or speculate on lease rates in the area; the BCPI is computed for cattle weighing over 227 kg (500 lbs) and does not include the lighter feeder calves produced on many western ranches; and the PPI excludes major feed expenses for western ranches. Kearl (1989), Brokken and McCarl (1987) and USDA/USDI (1986, 1992) provided additional detail about these and other criticisms and evaluated ways the indices could be changed and improved.

We start with the earlier statistical model defined by McCarl and Brokken (1985):

$$\text{FVI}_{t+1} = \beta_0 + \beta_1\text{FVI}_t + \beta_2\ \text{BCPI}_t + \beta_3\ \text{PPI}_t + u_t. \tag{1}$$

The beta coefficients are estimated regression parameters. Using this regression equation an estimate of the private land lease rate index during the next period (FVI_{t+1}) based on indexed values of private land lease rates, beef prices, and production costs during the current period can be made. As noted by McCarl and Brokken (1985, p. 775), the regression of current and lagged values is based on a normalization (indexing) of private land lease rate data. Predicting lease rates at year t +1 is equivalent to predicting FVI_{t+1} with normalization of the data. The error term (u_t) captures random differences in the FVI between years.

Dividing the predicted FVI_{t+1} (from equation 1) by 100 and multiplying by the 1964–1968 base lease rate used to estimate the FVI index (\$3.65 AUM^{-1}) gives the estimated private land lease rate at time t + 1. Similarly, because public land grazing fees should be less than private land lease rates when higher non-fee grazing costs for public lands are considered, equation 1 tracks public land grazing fees when the base fee rate is reduced. Multiplying by the \$1.23 AUM^{-1} Public Rangeland Improvement Act (PRIA) base (Table 1), for example, provides a grazing fee estimate during year t + 1 when the beta coefficients of equation 1 are not restricted. The PRIA formula implies the restrictions $\beta_0 = 0$, $\beta_1 = 1$, $\beta_2 = 1$, and $\beta_3 = -1$.

Several alternative statistical results are possible if the beta coefficients in equation 1 are varied and estimated using regression techniques. First, it may be that an equal unitary weighting should not be attached to each index, but with all 3 indices statistically important in predicting forage value. Second, the appropriate weighting for any particular index may not be statistically different from 1 and some indices may be statistically insignificant. As noted by Brokken and McCarl (1987,

p. 63), justification for PRIA would be evident if the implied restrictions of PRIA are not statistically significant (i.e., imposing the above restrictions does not significantly decrease the explanatory power of the model as measured by R^2).

The statistical significance of the PRIA restrictions was tested using restricted least squares regression. Using the residual sum of squares from the restricted (RSSR) and unrestricted (RSS_{UR}) models, the appropriate test statistic is given by an F-distribution with m and n-k degrees of freedom. The test statistic can also be formulated in terms of model R^2 values. The number of restrictions imposed, the number of observations and the number of parameters estimated in the unrestricted model are denoted by m, n, and k, respectively. The appropriate F-statistic can be computed as follows (Greene 1993):

$$F = \frac{(RSS_R - RSS_{UR})/m}{RSS_{UR}/(n-k)} \text{ or } \frac{(R^2_{UR} - R^2_R)/m}{R^2_{UR}/n-k)}. \quad \textbf{(2)}$$

Statistical significance of the F-statistic would suggest that at least 1 of the imposed model restrictions does not hold.

Using data defining annual values of the PRIA indices (Appendix A), equation 1 was first estimated with no restrictions imposed on the beta coefficients. This unrestricted model resulted in equations similar to those estimated by McCarl and Brokken (1985), Torell et al. (1989), Rimbey (1990), and Bartlett et al. (1993) to evaluate what parameter weighting should be attached to the PRIA indices to best predict forage value on a West-wide and state-level basis. These unrestricted regressions are now used to index state land grazing fees in Idaho and New Mexico (Rimbey 1990, Torell et al. 1989).

To test various restrictions on the estimated parameters, additional restricted models were evaluated using the TEST statement within PROC REG of SAS (Freund and Littell 1991). The first set of restrictions tested were that PRIA is an appropriate model formulation, or the null hypothesis of the first test, H_0: $\beta_0 = 0$, $\beta_1 = 1$, $\beta_2 = 1$, and $\beta_3 = -1$. A second test specified H_0 as $\beta_1 = 1$, $\beta_2 = 0$, and $\beta_3 = 0$ and was used to test whether the BCPI and PPI jointly added explanatory power to the model. This further tested whether only the lagged FVI variable should be used to predict FVI during the current period, similar to the original fee adopted in 1969 (USDI/USDA 1977).

Results

Using data from 1964–2001, the unrestricted Public Rangeland Improvement Act (PRIA) equation was estimated to be:

$$\begin{aligned} \hat{FVI}_t &= \underset{(10.572)}{4.5561} + \underset{(0.164)}{0.906^*} FVI_{t-1} \\ &+ \underset{(0.0476)}{0.085}\, BCPI_{t-1} + \underset{(0.08475)}{0.0085}\, PPI_{t-1} \quad \textbf{(3)} \end{aligned}$$

$R^2 = 0.985$, $\bar{R}^2 = 0.984$, n = 37.

The standard error of the estimate is in parentheses, with * signifying that the estimated parameter is individually statistically significant at the $\alpha = 0.05$ level. Only the lagged Forage Value Index (FVI) is statistically significant in the equation.

Durbin's h statistic was estimated to be –11.28, indicating autocorrelation ($P < 0.001$). White's test for heteroscedasticity did not indicate a significant problem ($P < 0.086$). Multicollinearity was a problem in the model. Data for the FVI, Prices Paid Index (PPI), and Beef Cattle Price Index (BCPI) variables were highly correlated ($r > 0.90$), which was not an unexpected result. As noted by McCarl and Brokken (1985), the FVI conceptually includes the other 2 variables because lessors of forage should consider livestock prices and production costs when formulating forage lease prices.

Testing the restrictions imposed by PRIA, using equation 2, resulted in a highly significant F-statistic (F = 1,526, $P < 0.0001$). This suggests that at least one of the restrictions implied by PRIA does not hold. The second test, H_0: $\beta_1 = 1$, $\beta_2 = 0$, and $\beta_3 = 0$, resulted in an insignificant F-statistic (F = 1.17, $P < 0.34$), suggesting that the PRIA restrictions that did not hold in the first test were the inclusion of the BCPI and PPI.

The equation suggested by the second statistical test is not exactly equal to the 1969 fee formula (i.e., $FVI_t = 1 \times FVI_{t-1}$). Rather, the equation includes a statistically insignificant intercept:

$$FVI_t = \underset{(4.88)}{6.6361} + \underset{(0.022)}{1.00} FVI_{t-1} \quad \textbf{(4)}$$

$R^2 = 0.984$, $= \bar{R}^2 = 0.983$

Additional restricted least squares analysis indicated that if the second test is modified to H_0: $\beta_0 = 0$, $\beta_2 = 0$, and $\beta_3 = 0$, such that the intercept is forced to 0 and the slope coefficient on lagged FVI is not fixed at 1, then the estimated slope coefficient for β_1 is 1.0285, and this slope coefficient is statistically different from one (F = 1.82, $P < 0.16$). This suggests that the nominal FVI grew by 2.85% per year over the study period[1], and should be considered when predicting annual changes in forage value:

$$FVI_t = \underset{(0.0075)}{1.0285} \times FVI_{t-1} \quad \textbf{(5)}$$

$R^2 = 0.998$, but redefined when forced through the origin

The results did not change when the AUM definition contained in the Executive Order (EO) was used to calculate FVI for all years (Appendix A). Conclusions of all statistical tests were identical. The estimated beta coefficients were slightly different, but statistically unchanged. The slope coefficient of equation 5, for example, increased to 1.0286 while the intercept term in equation 4 changed to 6.391. Similarly, the conclusions of the statistical tests and implications of the analysis remain unchanged relative to the earlier findings of McCarl and Brokken (1985).

Discussion

Adding the Beef Cattle Price Index (BCPI) and Prices Paid Index (PPI) to the Public Rangeland Improvement Act (PRIA) formula did not improve the fee formula's ability to predict annual forage values. In fact, adding these 2 indices ruined the predictive ability of the formula and PRIA-generated grazing fees have fallen further and further behind private land lease rates through time (Fig. 1). Similar to the earlier findings of McCarl and Brokken (1985), our results show that these 2 indices did not improve the ability of the fee formula to predict forage value and did not help explain short-term market imperfections as envisioned by the 1977 Grazing Fee Technical Committee. Including these 2 indices in the PRIA formula, especially with a weighting of 1, was a mistake if predictive power and tracking of the private forage market are important. Using a unitary weighting, while intuitive in a practical sense, does not give the correct coefficient in a statistical sense. The 1977 Grazing Fee Study stated that a desirable fee formula should prevent future discrepancies and adjust so that fair market value is charged in future years as well as the present (USDI/USDA 1977, p. 1-8). By this standard the PRIA formula has not been a desirable fee formula.

Had only the Forage Value Index (FVI) been used to adjust grazing fees (the 1969 fee formula), the federal grazing fee would have been \$4.15 AUM^{-1} during the 2002 grazing season. If equation 5 had been used, whereby growth in the FVI is recognized and expected, the 2002 fee would have been \$4.36 AUM^{-1} (Fig. 1). Fair market value of public land forage was estimated to be about 1/3 the private land lease rate (PLLR) during the 1964–1968 base period of PRIA (\$1.23 AUM^{-1} ÷ \$3.65 AUM^{-1} = 0.337). The \$4.36 AUM^{-1} fee obtained from equation 5 would represent nearly the same ratio of value in 2002 (\$4.36 AUM^{-1} ÷ \$12.30 AUM^{-1} average 2002 PLLR = 0.354). The fee would now be in the \$3 to \$5 AUM^{-1} range that was estimated to be "fair market value" during 1992 as part of a Grazing Fee Task Group assigned to advise BLM and FS on grazing fees (Bartlett et al. 1993). But, even with adjustment in the updating mechanism of the fee formula, value estimates for public land forage will remain controversial. There is no general agreement about the comparability of private and public land forage, nor is there agreement about what allowances and deductions should be credited to compensate for differences in forage quality, location, investments, and non-fee grazing costs (Kearl 1989).

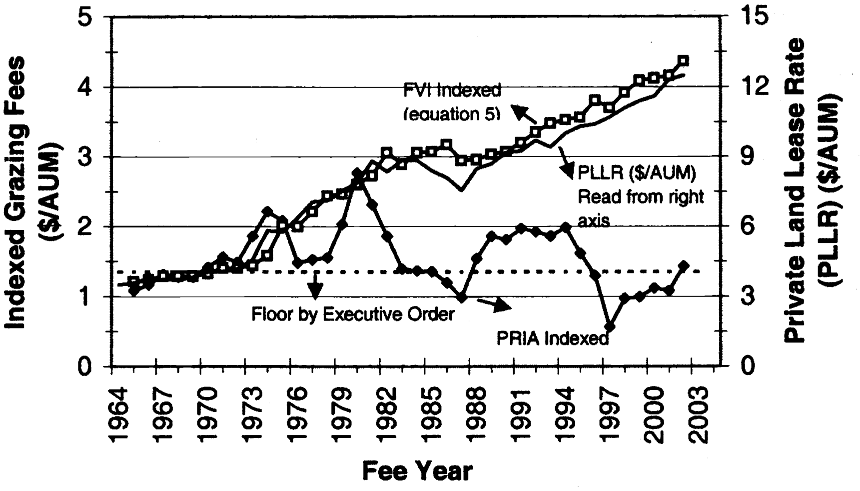

Fig. 1. Private land lease rates (\$ AUM^{-1}) compared with indexed grazing fees computed using the unrestricted Public Rangeland Improvement Act (PRIA) index and the Forage Value Index (FVI) from equation 5.

On the criterion of equity, the PRIA fee formula has been increasingly beneficial to public land ranchers if the historical precedent of not including interest on the grazing permit investment as a grazing cost is continued (USDI/USDA 1977, p. 3-8). It has been unfair to livestock producers that do not hold public land grazing permits, when judged against the criterion that an equitable fee should charge a similar amount as if the resource was used privately (USDI/USDA 1977, p. 1–8). If PRIA continues on the same general trend (Fig. 1), it is likely that the federal grazing fee will continue to be primarily determined by the \$1.35 AUM^{-1} floor set by Executive Order 12548, as it was for the 1995 through 2001 fee years.

One can only speculate about why the PRIA grazing fee formula has persisted for over 20 years. Economists pointed out problems of double counting with the formula even before it was implemented (Backiel and Rogge 1985). The poor tracking ability of the formula was identified before PRIA expired in 1985 (McCarl and Brokken 1985). Yet, the PRIA fee formula with Executive Order modification continues.

According to Darwin Nielsen, an agricultural economist actively involved with the grazing fee discussions as PRIA was adopted, political influence and pressure from public land ranchers played a significant role in the decision to include the BCPI and PPI in the PRIA fee formula (personal communication, Darwin B. Nielsen, Utah State University, retired, 10 October, 2000). Public land ranchers have actively lobbied to maintain the fee formula and perhaps the persistence of the formula can be attributed to their continued political activity and support.

Numerous grazing fee proposals have surfaced since the PRIA formula expiration date in 1985, including fee proposals studied in 1986 and updated in 1992 (USDA/USDI 1986, 1992). This was followed by the Incentive-Based Grazing Fee System in 1993 (USDI/USDA 1993), which was a study of grazing costs in Idaho, New Mexico, and Wyoming.

The Incentive-Based Fee Study was completed just as the Clinton administration came to Washington, D.C. The new administration started with an enthusiasm and desire to do something positive for the environment. Public lands were perceived to be in bad shape (USDI/USDA 1994, p. 5) and the new administration planned to reform grazing and mining regulations, and moved in a new direction that was called Rangeland Reform '94. Grazing fees and alternatives to improve rangeland health were considered in the draft Environmental Impact Statement (EIS) document (USDI/USDA 1994), but the focus eventually moved to rangeland health and fee reform was eliminated.

Grazing fee and management alternatives proposed in Rangeland Reform '94 were extremely controversial. The BLM and FS received over 20,000 comments to the draft EIS (USDI/USDA 1995). Efforts to change grazing fee policy under Rangeland Reform '94 were never completed. According to Lee Oteni, special assistant to the BLM Director and project leader for Rangeland Reform '94, BLM did not believe pursuing Rangeland Reform '94 management initiatives and increasing the grazing fee would be worth the necessary political capital (personal communication, 25 October, 2000).

Policy Implications and Alternatives

Differences in private land lease rates between states and regions (Tittman and Brownell 1984, Van Tassell and McNeley 1997, LaFrance and Watts 1995) and the widening difference between lease rates and public land grazing fees generated by using the PRIA grazing fee formula, have led researchers and policy analysts to different conclusions about how grazing fee policy should proceed. Nielsen (1972, p. 6) suggested that a competitive bid system would come closest to collecting full market value. Gardner (1963, 1983, 1989, 1997) argued that permittees should be given permanent rights to their grazing allotments. They should then be allowed to sell those rights to the highest bidder without restriction. He proposed that this disposal program might start with long-term competitive leases on an experimental basis and felt that the eventual privatization of the public lands would improve the efficiency of resource allocation (Gardner

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[1] Over the same study period the rate of inflation averaged 4.8% and average lease rates fell in real terms. McCarl and Brokken (1985) reported a similar regression coefficient for the earlier 1964–1983 period.

1983, p. 227). Similarly, LaFrance and Watts (1995) concluded public lands should be permanently transferred to the private sector. Whittlesey et al. (1993) would base grazing fees on the public cost of providing grazing in a multiple use framework. Fees would differ by grazing unit as acceptable stocking rates, grazing practices, and administrative costs vary.

While no uniform grazing fee recommendation has been made, perhaps a uniform message from this and previous research does emerge—the current PRIA-generated fee is inadequate. The fee formula has not met the objective of adjusting grazing fees through time so as to charge fair market value in current and future years (USDI/USDA 1977, p. 1–8). A growing disparity has arisen between private land lease rates and the public land grazing fee.

The \$1.35 AUM^{-1} grazing fee floor is where PRIA-generated grazing fees will likely remain in the future. It is a minimal grazing fee. But, there is no evidence that public land ranchers are subsidized and make an inflated rate of return because of low grazing fees. As noted by Martin and Jeffries (1966), Pope and Goodwin (1984), Workman (1988), Torell and Bailey (2000) and Bartlett et al. (2002), ranch properties are overpriced relative to their livestock earning potential. Private and public land ranchers have paid too much for western ranches and grazing permits based on the value of livestock production. At current grazing fee rates, or even with no grazing fees, public land ranchers will continue to make a rate of return below what could be made from alternative investments of similar risk (Torell and Bailey 2000, Torell et al. 2001, Bartlett et al. 2002). Inflated ranch prices and grazing permit investments demonstrate that public land ranchers are willing to pay more than the current grazing fee to graze public lands.

There seems to be general agreement that, to discover allotment-specific forage values, we must either establish a market for public land grazing through privatization of public lands or by determining lease prices with a competitive bid system. A competitive bid system has strong theoretical appeal, and it has been proposed and studied numerous times in the past (Nielsen 1972, Martin and Jeffries 1966, USDI/USDA 1977, USDA/USDI 1992). However, the option of moving to a competitive bid system has been repeatedly rejected by the federal land agencies. They believe it would be disruptive to the stability of permittees and rural communities

APPENDIX A

Indices used to compute PRIA grazing fees

Reporting Year	Fee Year	FVIAUM[a]	FVIHEAD[a]	FVIPRIA[a]	BCPI	PPI
1964	1965	96		96	87	95
1965	1966	98		98	94	97
1966	1967	102		102	104	99
1967	1968	102		102	105	103
1968	1969	102		102	109	107
1969	1970	105		105	123	113
1970	1971	111		111	134	118
1971	1972	111		111	134	124
1972	1973	114		114	167	130
1973	1974	125		125	195	140
1974	1975	159		159	178	168
1975	1976	158		158	160	198
1976	1977	175		175	164	215
1977	1978	193		193	163	230
1978	1979	195		195	216	246
1979	1980	206	200	206	294	275
1980	1981	216	233	216	291	319
1981	1982	242	241	242	268	359
1982	1983	229	248	229	262	378
1983	1984	242	236	242	256	387
1984	1985	243	242	243	262	395
1985	1986	230	251	251	243	397
1986	1987	222	233	233	235	388
1987	1988	207	234	234	272	381
1988	1989	233	240	240	297	386
1989	1990	238	243	243	306	402
1990	1991	252	253	253	326	419
1991	1992	253	265	265	327	436
1992	1993	266	275	275	316	440
1993	1994	258	279	279	333	451
1994	1995	274	282	282	304	455
1995	1996	282	301	301	277	473
1996	1997	285[a]	293	293	252	499
1997	1998	293	310	310	281	512
1998	1999	304	323	323	323	272
1999	2000	312	326	326	326	281
2000	2001	318	329	329	329	313
2001	2002	337	345	345	345	330

Source: USDA/USDI (1992, p. 18) and updated values reported in USDA-NASS *Agricultural Prices* (Various Issues).

[a] /The PRIA fee formula expired with the 1986 fee year, and Executive Order 12548 mandated that the FVI be defined as the per head per month rate for pasturing cattle on private rangelands in the 11 western states. This was a redefinition relative to the per AUM definition previously used. The FVIPRIA column includes this redefinition, beginning with the 1986 fee year.

dependent upon public land forage, and would not be manageable given the isolated and scattered nature of many public lands grazing permits, especially with current permit structure, regulation, and staffing (USDI/USDA 1977, p. 7-7, USDA/USDI 1992, p. 40, USDI/USDA 1993, p. 15). No effort has been undertaken to seriously evaluate the feasibility of moving to a competitive bid system on public lands. As noted by the land agencies, scattered and isolated allotments create obstacles for having multiple and competitive bids submitted under an open eligibility bidding system. But, in many cases, market-driven competitive bids and lease rates could be obtained. Average bid rates for selected areas or grazing districts could then be used to set fees for tracts for which a competitive bid was not possible.

Competitive bidding on lands administered by BLM has occurred on a very limited basis on the McGregor Bombing Range in southern New Mexico and at Fort Meade in South Dakota (USDA/USDI 1992, Fowler et al. 1994). Competitive bids are also allowed on state trust lands in many western states (Baldwin and Cody 1996). These leases have recently been controversial as environmental groups have offered bids in an attempt to preclude grazing on state lands. The question of bidding procedure and qualified bidders are details that would have to be addressed prior to instituting an expanded bidding system for public lands. Perhaps more important is the question of whether a competitive bidding process would be politically possible, socially acceptable and economically justified. As noted by McCarl and Brokken (1985, p. 777), the desirability of moving to a competitive bid system will ultimately depend on transaction and administrative costs that will occur under a bidding program. Other key issues include the desire for simplicity, the feasibility and need to alter current rules and regulations to open and expand the number of eligible bidders, and equity concerns about who gains and loses as grazing policies change. McCarl and Brokken (1985) expressed a concern that the data needed to implement a competitive bid system will not be forthcoming and question whether its social value would be worth the costs incurred in its development. While recognizing the potential validity of these concerns, and those of the land agencies, we believe the competitive bid option warrants additional study and serious consideration.

If McCarl and Brokken (1985, p. 777) are correct such that we must settle for a somewhat arbitrary institutionalized system for setting grazing fees, the Public Rangeland Improvement Act (PRIA) evaluation presented here has several clear implications for the development of a new fee system. Clearly, the Beef Cattle Price Index (BCPI) and Prices Paid Index (PPI) should be discarded when judged against the criteria of preventing future discrepancies in grazing fees. Van Tassell and McNeley (1997) have documented that beef prices and production costs are adequately captured in the Forage Value Index (FVI), as economists argued was the case when decisions were originally made to include the BCPI and PPI in the PRIA fee formula. Further, as demonstrated by McCarl and Brokken (1985) and this update, adding these 2 indices did not improve the tracking ability of the PRIA fee formula as was originally envisioned, and, in fact, had exactly the opposite effect.

Perhaps the best estimate of what private forage will lease for next year is what it leased for this year. The lagged FVI has proven to track private land lease rates through time (Fig. 1). It likely does not matter whether per AUM or per head rates are used in defining the FVI and there is always room to improve the lease rate data collection process and expand sample size. The weighting of the lagged FVI could be one (1), but an improved tracking could be obtained by recognizing that nominal forage values are expected to grow over time. Efficient pricing of public forage on a site-specific basis will be more complicated and may require data collection and administrative costs that would not be justified from grazing values.

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J. Range Manage.
56: 585–590 November 2003

Roller chopping effects on tamaulipan scrub community composition

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Abstract

Palatability of shrub sprouts to white-tailed deer (*Odocoileus virginianus* Raf.) differs among species, which causes selective browsing and can shift shrub species composition to dominance by less palatable species. The hypothesis was tested that differences in palatability of new sprouts among shrub species following roller chopping small (4 ha) patches within a shrubland matrix would result in a shift in shrub species composition within the patches toward less palatable species. Relative density and relative canopy cover of all woody species in plots 9 years after 1 roller chopping treatment, in plots 3 years after 2 roller chopping treatments, and in untreated plots were estimated. Relative density of blackbrush acacia (*Acacia rigidula* Benth.) was 3 times greater and relative canopy cover was 12 times greater 9 years after the first roller chopping treatment compared to untreated plots, but relative density and relative canopy cover of blackbrush acacia in roller chopped plots were similar to relative density and relative canopy cover in untreated plots 3 years after the second roller chopping treatment. Relative canopy cover of spiny hackberry (*Celtis pallida* Torr.) in plots roller chopped in 1989 and 1995 was higher than in untreated plots. Relative density and canopy cover of all other species were similar between roller chopped and untreated plots. Shrub community composition 9 years after 1 roller chopping treatment or 3 years after 2 roller chopping treatments in the subtropical thornscrub communities in southern Texas did not shift toward greater dominance of less palatable species.

Resumen

La palatabilidad de los rebrotes de diferentes arbustos para el venado cola blanca (*Odocoileus virginianus* Raf.) difiere entre distintas especies, lo cual causa ramoneo selectivo de los venados y puede provocar la dominancia de las especies menos palatables. La hipótesis probada fue que las diferencias en palatabilidad de rebrotes entre especies de arbustos después del roleo de pequeñas áreas (4 ha) dentro de el matorral resultaría en un cambio en la composición de las especies de arbustos en las áreas roleadas favoreciendo las especies menos palatables. Se estimó densidad relativa y cobertura aérea relativa para todas las especies arbustivas en las parcelas roleadas 9 años después de 1 tratamiento de roleo, 3 años después de 2 roleos, y en parcelas sin rolear (testigo). La densidad relativa y la cobertura relativa de chaparro prieto (*Acacia ridigula* Benth.) fue 3 y 12 veces superior, respectivamente, al tratamiento testigo, sin embargo, las mismas variables reapuesta fueron similares para el tratamiento testigo y el tratamiento de 2 roleos 3 años después del segundo roleo. La cobertura relativa de granjeno (*Celtis pallida* Torr.) en las parcelas que se rolearon en 1989 y 1995 fue superior que en el tratamiento testigo. La densidad relativa y cobertura aérea de todas las demás especies arbustivas fueron similares entre los tratamientos de roleo y el testigo. La composición de la comunidad arbustiva 9 años después del un tratamiento de roleo o 3 años después de 2 roleos en comunidades de matorral espinoso subtropical en el Sur de Texas no provocó una mayor dominancia de las especies menos palatables.

Key Words: *Acacia rigidula*, blackbrush acacia, brush management, *Celtis pallida*, spiny hackberry, white-tailed deer

Many shrub species produce sprouts from stems, crowns, and roots to replace above-ground tissue removed by roller chopping, mowing, and other top-growth removal treatments (Scifres 1980, Fulbright and Taylor 2001). Top growth removal of woody plants in small patches within a surrounding matrix of shrubland results in intense browsing on newly-produced sprouts by white-tailed deer (*Odocoileus virginianus* Raf.) (Stewart et al. 2000). White-tailed deer concentrate feeding activity in clearings created by mechanical top removal and may travel from adjacent areas to utilize habitats with clearings (Naderman 1979, Bozzo et al. 1992). White-tailed deer fecal-group density averaged 8 times higher in 30 to 125 ha clearings created by shrub top growth removal than in adjacent uncleared shrubland (Bozzo et al. 1992). Intensive use by white-tailed deer of patches created by top growth removal is partly a result of the presence of new sprouts produced by shrubs (Stewart et al. 2000). Sprouts temporarily contain higher nutrient levels and are more accessible to herbivores than the canopy of mature, untreated plants (Scifres 1980, Vallentine 1980, Yoakum et al. 1980).

Not only are patches created by top removal more heavily used by deer, but certain shrub species are more palatable after top removal than others, resulting in intense browsing pressure on the palatable shrubs. Relative preference of spiny hackberry (*Celtis pallida* Torr.), brasil (*Condalia hookeri* M. C. Johnst.), and agari-

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Research was funded by the Rob and Bessie Welder Wildlife Foundation and the Caesar Kleberg Foundation for Wildlife Conservation. This is publication number 584 from the Rob and Bessie Welder Wildlife Foundation and publication number 02-111 from the Caesar Kleberg Wildlife Research Institute.

Manuscript accepted 23 Dec. 02.

to [*Mahonia trifoliolata* (Moric.) Fedde], increased 13,217%, 2,221%, and 1,758%, respectively, after top growth removal (Powell and Box 1966). In contrast, relative preference of blackbrush acacia (*Acacia rigidula Benth.*), huisache (*A. smallii* Isely), Texas persimmon (*Diospyros texana* Scheele), and twisted acacia [*A. schaffneri* (S. Wats) Herm.] each decreased 71%.

Differences in palatability induce selective browsing by herbivores (Westoby 1974, Bryant et al. 1991), which in turn mediates the impacts of herbivory on plant species populations (Illius et al. 1999) and on shrub community composition. Less palatable species theoretically should have a competitive advantage over highly palatable species that are continually browsed by herbivores and should increase in relative abundance in the plant community (Bryant et al. 1991).

Repeated defoliation of guajillo (*Acacia berlandieri* Benth.) results in mortality of the defoliated stems (Forbes et al. 1995). Repeated removal of photosynthetic tissue from sprouts produced to replace aboveground parts removed by mechanical means may inhibit survival and re-establishment of highly palatable shrubs. Because preference of shrub sprouts differs dramatically from preference of mature untreated plants, and because the amplitude of these differences varies among species, top growth removal may shift the shrub community composition to dominance by less palatable species because of increased browsing pressure on highly palatable species and reduced browsing pressure on less palatable species. Decreased shrub species diversity 7 to 30 years after mechanical top growth removal has been reported (Fulbright 1987, Fulbright and Beasom 1987), but the mechanisms explaining the loss of species remain unclear.

The hypothesis was tested that the long-term result of roller chopping small (4 ha) patches within a shrubland matrix would be a shift in shrub species composition within the patches. Roller chopping was predicted to result in increased relative density and relative canopy cover of species reported to have lowered relative preference after top growth removal (Powell and Box 1966), while species highly preferred after top growth removal were predicted to decrease in relative density and relative canopy cover after roller chopping.

Materials and Methods

Study Area

The study was conducted on the Rob and Bessie Welder Wildlife Foundation Refuge, which consists of 3,158 ha of native rangeland 70 km north of Corpus Christi in San Patricio County, Tex. (28° 6' 49"N, 97° 25' 00"W). The refuge lies adjacent to the Aransas River at about 12 m above sea level, with a slope gradient $< 1\%$. Climate is characterized as subtropical with hot summers and mild winters (Box 1961). Average length of the frost-free growing season was 300 days. The average annual maximum and minimum temperatures (1982 to 1998) were 27 and 17° C, respectively (Rob and Bessie Welder Wildlife Foundation, Refuge Records). Average annual rainfall (1956 to 1998) recorded on the refuge was 89 cm, with bimodal peaks occurring in spring and fall. Average rainfall from 1989 through 1997 was 84 cm, 94% of the annual average. Average rainfall from 1995 through 1997 was 85 cm, 95% of the annual average.

Two major plant communities were present in the study area: a chaparral-mixed grass community, with a variety of dominant shrub species, and a live oak-chaparral community dominated by live oak (*Quercus virginiana* Mill.), with a shrub community similar in species composition to the chaparral-mixed grass community (Drawe et al. 1978). Soils included Victoria clay (Udic Pellustert), Papalote fine sandy loam (Aquic Paleustalf), Orelia fine sandy loam (Typic Ochraqualf), and Orelia sandy clay loam (Typic Ochraqualf) (Guckian and Garcia 1979). The study area averaged 26 ± 3 (0 mean ± SE, n = 21) individual white-tailed deer per km^2 (Rob and Bessie Welder Wildlife Foundation Refuge Census Records, 1975 to 1995).

Experimental Design

A randomized, complete-block design (blocking based on soil differences) with each block (replicate) consisting of a 4-ha (100 x 400 m) roller chopped plot and an adjacent 4-ha untreated plot selected randomly east or west of the roller chopped plot was used in the study. A roller chopper is a large cylindrical metal drum with metal blades mounted parallel to its axis. The roller chopper is pulled by a crawler tractor and severs stems of woody plants, with up to 6-in diameters, at the soil surface. Four blocks contained treatment plots that were roller chopped once in 1989 and untreated control plots. Five blocks contained treatment plots that were roller chopped twice, in 1989 and in 1995, and untreated control plots. Data from plots roller chopped once in 1989 and adjacent controls, and data from plots roller chopped twice, in 1989 and 1995, and adjacent controls were analyzed as 2 separate randomized, complete-block experiments. All measurements were taken in 1998, 9 years after the first roller chopping treatment and 3 years after the second roller chopping treatment.

Data Collection and Analysis

Density and percentage canopy cover estimates were made during June 1998 in plots roller chopped in 1989 and in corresponding untreated plots to determine long-term (9 years after 1 roller chopping treatment) effects of roller chopping on shrub community composition. Density and percentage canopy cover estimates in plots roller chopped in both 1989 and 1995 and in corresponding untreated plots were made during February 1998 (3 years after the second roller chopping treatment). Densities of all shrub and half-shrub species [nomenclature follows Hatch et al. (1990)] were estimated by counting the number of individual plants rooted in 12, 1x10-m belt transects located perpendicular to each side of the common boundary of roller chopped and untreated plots. An individual plant consisted of a distinct group of sprouts originating from basal crowns of multi-stemmed species, or ramets originating from lateral roots. Transects were placed randomly between 10 and 90 m from each side of the boundary. Percentage canopy cover of each shrub and half-shrub species was estimated with the line-intercept technique (Canfield 1941) along a 10-m line transect at the south border of each belt transect.

Density and percentage canopy cover data were converted to relative density and relative canopy cover by dividing the absolute density and canopy cover for each species by the total density and canopy cover of all species combined within each experimental unit. Relative density and relative canopy cover for each species were compared between roller chopped and untreated plots using analysis of variance (ANOVA) for a randomized, complete-block design with treatment as the main effect (SAS Institute, Inc. 1989). The outcome of analyses of variance with arcsine transformed relative density and canopy cover means was similar to the outcome with non-transformed values, so statistical analyses were conducted with non-transformed values. Differences were considered significant at the 0.05 level.

Species composing <1% of the shrub community in both the roller chopped and untreated plots were not included in comparisons. Linear regression was used to determine the relationship between changes in relative densities of shrub species after roller chopping and changes in relative preference after top growth removal based on preference values reported in Powell and Box (1966). The change in relative preference for each species was calculated by subtracting the relative preference of a species after mowing from the relative preference of the species in untreated plots and dividing the result by the relative preference of the species in untreated plots. In the current study, the change in relative density of each species was calculated by subtracting the relative density of a species in roller chopped plots from the relative density of the species in untreated plots and dividing the result by the relative density of the species in untreated plots.

Table 1. Scientific and common names of all shrub and half-shrub species recorded in the shrub community on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Tex., 1998. Nomenclature follows Hatch et al. (1990).

Scientific name	Common name
Acacia rigidula Benth.	Blackbrush acacia
Acacia smallii Isely	Huisache
Amyris texana (Buckl.) P. Wils.	Chapatillo
Bumelia lanuginosa (Michx.) Pers.	Coma
Celtis pallida Torr.	Spiny hackberry
Condalia hookeri M. C. Johnst.	Brasil
Diospyros texana Scheele	Texas persimmon
Forestiera angustifolia Torr.	Narrowleaf Forestiera
Guaiacum angustifolium Engelm.	Guayacan
Lantana horrida Kunth. In H.B.K.	Common lantana
Lycium berlandieri Dunal	Berlandier wolfberry
Mahonia trifoliolata (Moric.) Fedde	Agarito
Opuntia leptocaulis DC.	Tasajillo
Opuntia lindheimeri Engelm.	Texas prickly pear
Parkinsonia aculeata L.	Retama
Prosopis glandulosa Torr.	Honey mesquite
Quercus virginiana Mill.	Live oak
Yucca treculeana Carriere	Spanish dagger
Zanthoxylum fagara (L.) Sarg.	Lime pricklyash
Zizyphus obtusifolia (T. & G.) Gray	Lotebush

Results

Relative Density

Twenty woody species were recorded in roller chopped and untreated plots (Table 1). Blackbrush acacia, brasil, honey mesquite, huisache, lime pricklyash, spiny hackberry, and Texas persimmon composed 88 ± 18% and 82 ± 31% (mean ± SE, n = 4) of the shrub community in plots roller chopped in 1989 and in untreated plots, respectively (Table 2). Relative density of blackbrush acacia was 3 times higher ($P = 0.005$) in plots roller chopped in 1989 compared to untreated plots. Relative densities of all other recorded species, regardless of relative preference after top growth removal, were similar ($P > 0.05$) between roller chopped and untreated plots. There was no significant linear relationship ($R^2 = 0.004$, $P = 0.879$) between changes in relative densities of shrub species 9 years after 1 roller chopping treatment and changes in relative preference after top growth removal, based on preference values reported by Powell and Box (1966).

Blackbrush acacia, brasil, honey mesquite, huisache, lime pricklyash, spiny hackberry, and Texas persimmon composed 87 ± 22% and 74 ± 18% (mean ± SE, n = 5) of the shrub community on plots roller chopped in 1989 and 1995 and on untreated plots, respectively. Relative densities of all shrub and half-shrub species on roller chopped and untreated plots were similar ($P > 0.05$) 3 years after the second roller chopping treatment. There was no significant linear relationship ($R^2 = 0.34$, $P = 0.100$) between changes in relative densities of shrub species 3 years after 2 roller chopping treatments and changes in relative preference after top growth removal, based on preference values reported by Powell and Box (1966).

Relative Canopy Cover

Absolute canopy cover of shrubs did not differ ($P = 0.554$) between plots roller chopped in 1989 (78 ± 7%) and untreated plots (81 ± 2%). Absolute woody canopy cover in plots roller chopped in 1989 and 1995 (35 ± 6%) was lower ($P = 0.006$) than in untreated plots (71 ± 8%). Relative canopy cover of blackbrush acacia in plots roller chopped in 1989 was significantly higher ($P = 0.006$) than in untreated plots (Table 3), which corresponded with the increase in relative density of blackbrush acacia in plots roller chopped in 1989. Relative canopy cover of spiny hackberry in plots roller chopped in 1989 and 1995 was greater ($P = 0.025$) than in untreated plots. Relative canopy cover of all other shrub species was similar ($P > 0.05$) between roller chopped and untreated plots.

Discussion and Conclusions

Shrub community composition 9 years after 1 roller chopping treatment and 3 years after 2 roller chopping treatments could not be predicted based on changes in relative preference reported by Powell and Box (1966) after top growth removal. The only exception was that blackbrush acacia, a species that decreased in relative preference after top growth removal, composed a larger percentage of the shrub community 9 years after 1 roller chopping treatment compared to untreated communities. Roller chopping on the Welder Wildlife Refuge reduced overall shrub canopy cover for at least 3 years but not for 9 years, which supports earlier reports that shrub canopy cover is decreased for only 2 to 3 years after roller chopping (Welch et al. 1985, Bozzo et al. 1992).

There are several possible reasons why changes in relative preference after top growth removal failed to predict long-term shrub community composition after roller chopping in the subtropical thornscrub of southern Texas. First, shrub sprouts produced following top removal are more palatable than browse from untreated plants only for a short time following top removal. Stewart et al. (2000) attributed increased white-tailed deer use of areas on the Welder Wildlife Refuge immediately after roller chopping to the presence of lush shrub sprouts. However, deer use of these areas declined as the sprouts matured, thus alleviating browsing intensity. Palatability of newly-produced sprouts declines rapidly. For example, sprouts from burned spiny hackberry plants were browsed more heavily than twigs from unburned plants for only 9 weeks after a

Table 2. Mean values[1] of relative density (%) of all shrub and half-shrub species in plots that were roller chopped once in 1989 (n = 4 plots per treatment) and twice, in 1989 and in 1995 (n = 5 plots per treatment), compared to untreated plots on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Tex., 1998.

		1989					1989 and 1995				
Species	Preference[2]	Roller chopped		Untreated			Roller chopped		Untreated		
		(%)	SE	(%)	SE	P	(%)	SE	(%)	SE	P
Honey mesquite	17	25	6	35	13	0.325	23	7	37	7	0.156
Lime pricklyash	192	16	2	18	3	0.109	23	3	13	4	0.074
Blackbrush acacia	-71	16	3	5	4	0.005	8	3	4	2	0.141
Spiny hackberry	13,217	12	3	7	3	0.180	14	4	6	1	0.135
Texas persimmon	-71	7	1	7	3	0.963	4	1	3	1	0.730
Huisache	-59	6	1	6	3	0.982	9	3	7	2	0.735
Brasil	2,221	6	2	4	2	0.601	6	1	4	1	0.246
Lotebush	31	5	3	1	1	0.266	1	1	1	1	0.700
Agarito	1,758	3	1	3	2	0.960	3	1	4	2	0.693
Chapatillo	NR[3]	3	1	7	3	0.280	<1	<1	2	1	0.388
Tasajillo	NR	2	1	5	4	0.547	1	1	6	4	0.296
Texas prickly pear	NR	1	<1	<1	<1	0.884	1	1	1	1	0.843
Narrowleaf forestiera	NR	<1	<1	3	2	0.240	<1	<1	1	1	0.178
Berlandier wolfberry[4]	NR	<1	<1	<1	<1		3	1	5	1	0.354
Live oak[4]	NR	0		0			4	4	0		0.374
Retama[4]	NR	0		0			0		3	3	0.334
Coma[4]	NR	0		0			0		1	1	0.374
Common lantana[4]	NR	0		0			<1	<1	<1	<1	
Guayacan[4]	NR	0		0			<1	<1	0		

[1] Data were analyzed using analysis of variance (ANOVA) for a randomized complete block design.

[2] Change in relative preference (%) for white-tailed deer and cattle during the first growing season after mowing. Powell and Box (1966) calculated preference values of shrub species in untreated plots and after mowing by multiplying percent utilization by frequency of use at a deer density of 1 deer per 2.4 ha. In the current study, relative preference of each species was calculated from those preference values by dividing the preference value of a species by the sum of the preference values of all species reported. The change in relative preference for each species was calculated by subtracting the relative preference of a species after mowing from the relative preference of the species in untreated plots and dividing the result by the relative preference of the species in untreated plots.

[3] NR = Not reported by Powell and Box (1966).

[4] Species with relative density <1% in roller chopped and untreated plots were not analyzed.

Table 3. Mean values[1] of relative canopy cover (%) of all shrub and half-shrub species in plots that were roller chopped once in 1989 (n = 4 plots per treatment) and twice, in 1989 and in 1995 (n = 5 plots per treatment), compared to untreated plots on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Tex., 1998.

	1989					1989 and 1995				
Species	Roller chopped		Untreated			Roller chopped		Untreated		
	(%)	SE	(%)	SE	P	(%)	SE	(%)	SE	P
Honey mesquite	35	5	50	5	0.205	32	6	45	9	0.107
Lime pricklyash	15	2	14	3	0.959	16	2	11	3	0.311
Blackbrush acacia	12	2	1	1	0.006	9	3	5	2	0.222
Spiny hackberry	11	3	7	2	0.209	12	2	2	1	0.025
Texas persimmon	8	2	9	4	0.751	4	1	5	2	0.494
Huisache	7	3	5	3	0.751	9	4	13	1	0.287
Brasil	9	2	10	2	0.824	9	3	9	3	0.962
Lotebush[2]	<1	<1	<1	<1		<1	<1	<1	<1	
Agarito	2	1	2	1	0.996	3	1	2	1	0.561
Chapatillo[2]	<1	<1	1	<1	0.596	<1	<1	<1	<1	
Tasajillo	1	<1	<1	<1	0.210	<1	<1	3	3	0.416
Texas prickly pear[2]	1	1	0		0.391	<1	<1	<1	<1	
Narrowleaf forestiera	<1	<1	2	1	0.256	1	1	<1	<1	0.411
Berlandier wolfberry[2]	0		0			1	1	2	1	0.565
Live oak[2]	0		0			1	1	0		0.374
Retama[2]	0		0			0		1	1	0.374
Common lantana[2]	0		0			<1	<1	0		
Coma[2]	0		0			0		<1	<1	
Guayacan[2]	0		0			<1	<1	0		
Spanish dagger[2]	0		0			<1	<1	0		

[1] Data were analyzed using analysis of variance (ANOVA) for a randomized complete block design.

[2] Species with relative canopy cover <1% in roller chopped and untreated plots were not analyzed.

prescribed fire (Schindler 2000). White-tailed deer on the Welder Wildlife Refuge consume a diverse diet that is dominated by forbs and use browse heavily only during periods of drought and low herbaceous plant availability (Chamrad and Box 1968, Drawe 1968). Therefore, even with the temporary increase in browsing intensity in cleared patches, browsing by deer may not be intense enough to significantly impact populations of highly palatable shrubs.

Second, the ability to tolerate or resist browsing following top growth removal may prevent shrubs that are highly palatable after top growth removal from being damaged by herbivory. Most of the shrub species in our study produce sprouts from crowns and roots after mechanical top growth removal (Scifres 1980, Scifres and Hamilton 1993), resulting in plants with multiple stems. In this way, the shrubs can actually increase biomass production and reduce the impacts of herbivory because the biomass eaten relative to the available biomass decreases. Density of shrub species in boreal forests of Isle Royale National Park was unaffected by moose browsing, possibly because of their ability to increase basal sprouting and develop lateral buds after apical dominance was disturbed by browsing (Snyder and Janke 1976). Increased stem production may create the potential for long-term increased seed production. Long-term density of highly palatable browse species after top growth removal may not decrease in part because of increased seed production and subsequent juvenile recruitment.

Although spiny hackberry is highly palatable to white-tailed deer, this species has been described as an invader following brush management (Scifres et al. 1976, Drawe 1977) and may increase in shrub community composition after top growth removal (Box and Powell 1965, Fulbright and Beasom 1987). Spiny hackberry increases stem production after top growth removal (Asah et al. 1987, Flinn et al. 1992), which probably helps protect this species from decreasing in abundance after roller chopping. In addition, the shrub appears to be highly tolerant of defoliation. Standing crop of spiny hackberry leaves and stems 13 months after top growth removal was unaffected by complete removal of regrowth at 3 and 6 months after top growth removal (Asah et al. 1987).

Third, juvenile stages of many shrubs are more protected by chemical and physical antiherbivore defenses than the conspecific mature stage (Bryant and Julkunen-Tiitto 1995). Juvenile quaking aspen (*Populus tremuloides* Michx.) plants in the Great Basin of North America are more chemically defended than mature plants (Basey et al. 1988). Juvenile plants of Alaska paper birch (*Betula papyrifera* Marsh) have high concentrations of certain terpene resins that are not present in mature plants (Reichardt et al. 1984). If juvenile stages of south Texas shrub species have increased antiherbivore defenses, then densities of shrub species may not be altered by top growth removal and subsequent herbivory. Removing top growth of mature shrubs can cause reversion to the more heavily defended juvenile stage (Chapin et al. 1985, Bryant et al. 1992). Fresh regrowth of shrubs after roller chopping may invest more into chemical and physical defenses. Sprouts produced by guajillo (*Acacia berlandieri* Benth.) after pruning have higher concentrations of tyramine and N-methyl-β-phenethylamine than mature growth (Forbes et al. 1995).

Mammalian herbivory in general will not cause high mortality of woody species once they have been established, with possible exceptions occurring under intense herbivory on low-productivity sites (Edenius et al. 1995). Relative preference after top growth removal might be a better predictor of shrub community composition in more arid areas where productivity is low, herbaceous vegetation is sparse, and shrubs compose a large percentage of white-tailed deer diets. Browse species composed 94% of annual deer diets in Nuevo Leon in northeastern Mexico, with blackbrush acacia composing 51% of diets (Ramirez et al. 1996). Blackbrush acacia composed 17.3% of the shrub community in Ramirez et al. (1997), while palatable species such as spiny hackberry and brasil composed only 0.7% and 0.6%, respectively, of the shrub community. Implementing top growth removal techniques in more arid areas may impact the shrub community more adversely than managing brush in more productive sites like the Welder Wildlife Refuge.

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J. Range Manage.
56: 591–599 November 2003

Growth and reproductive responses of true mountain mahogany to browsing

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Abstract

True mountain mahogany (*Cercocarpus montanus* Raf.) compensates for annual growth lost to browsing under conditions of high resource availability. To develop better guidelines for its management for big game winter forage, twig demography was studied under natural herbivory and resource availability inside and outside exclosures at 1 site in the Wasatch Mountains and on 4 sites on the North Slope of the Uinta Mountains, Utah. Annual and previous years' twig lengths, as well as location and numbers of flowers and seeds were diagrammed on branches of browsed and unbrowsed shrubs in the spring or summer and fall between 1996 and 1999. Annual twig growth and flower and seed numbers of both browsed and unbrowsed shrubs were greatest in 1997 or 1998 when precipitation was highest. Utilization of annual growth varied among sites within a year and among years within a site and ranged from < 21 % to > 300 % when previous years' growth was browsed. Despite differences in utilization, browsed twigs compensated similarly for length lost to herbivory, so that total twig lengths remained the same over the course of the study. Although twigs on unbrowsed shrubs had less annual growth per unit branch length than those on browsed shrubs, lack of length lost to herbivory resulted in an increase in total twig length over time. Years of high resource availability are important in allowing grazing tolerant shrubs such as true mountain mahogany to compensate for years of heavy utilization. Flower and seed numbers were much higher ($P < 0.05$) on unbrowsed than browsed shrubs. Compensatory growth was enough to maintain, but not increase total twig lengths after high utilization (> 100 %) even on years of high resource availability.

Key Words: twig demography, utilization, grazing optimization, compensatory growth, herbivory, shrubs, Utah, mountain brush, exclosures, *Cercocarpus montanus*

Resumen

Bajo condiciones de alta disponibilidad de recursos el "True mountain mahogany" (*Cercocarpus montanus* Raf.) compensa la perdida del crecimiento anual debido al ramoneo. Para desarrollar mejores guías para su manejo para producir forraje en invierno para la fauna silvestre mayor se estudio la demografía de las ramillas bajo herbivoría natural y disponibilidad de recursos dentro y fuera de exclusiones en un sitio en las montañas de Wasatch y en 4 sitios en la exposición norte de las montañas Uinta, Utah. La longitud anual, y la del año previo, de las ramillas, así como su localización, número de flores y semillas fueron diagramatizadas en ramas de arbustos con y sin ramoneo durante la primavera o verano y otoño entre 1996 y 1999. El crecimiento anual de las ramillas y el número de flores y semillas de arbustos tanto ramoneados como no ramoneados fueron mayores en 1997 o 1998 cuando la precipitación fue la mayor. La utilización del crecimiento anual varió entre sitios dentro del año y entre años dentro de un sitio, y fluctuó de <21% a >300% cuando el crecimiento del año previo fue remoneado. A pesar de las diferencias en utilización, las ramillas ramoneadas compensaron la longitud perdida por herbivoría tal que la longitud total de la ramilla permaneció igual a través del curso del estudio. Aunque las ramillas de los arbustos no ramoneados tuvieron menos crecimiento anual por unidad longitud de la ramilla que las de los arbustos ramoneados, la falta de perdida de longitud por herbivoría resultó en un incremento de la longitud total de la ramilla través del tiempo. Años con una alta disponibilidad de recursos son importantes para permitir a los arbustos tolerantes al ramoneo, tal como el "True mountain mahogany", compensar los años de utilización fuerte. El número de flores y semillas fueron mucho mayores ($P < 0.05$) en los arbustos sin ramoneo que en los ramoneados. El crecimiento compensatorio fue suficiente para mantener, pero no incrementar, la longitud total de las ramillas después de una alta utilización (> 100 %) aun en años de alta disponibilidad de recursos.

True mountain mahogany (*Cercocarpus montanus* Raf.) is one of the most important browse species in the mountain brush zone (Holechek et al. 2001), and is considered tolerant of browsing (Shepherd 1971, Davis 1990). Low growth form and basal sprouting allow big game easy accessibility to its forage (Davis 1990). On the North Slope of the Uinta Mountains, it has been heavily used in winter primarily by moose (*Alces alces*) and elk (*Cervus elaphus*), but also by deer (*Odocoileus hemionus*) or pronghorn antelope (*Antilocapra americana*) (Turley et al. 2003). In that study, heavy browsing reduced canopy cover and shrub size of true mountain mahogany, but shrubs on some sites with over 300 % utilization of annual growth still maintained their size.

The grazing optimization hypothesis proposes that at a certain grazing intensity, production is optimized (Briske and Heitshmidt 1991). An important basis for this hypothesis is that plants can compensate for tissue lost to herbivory, and that growth may even be stimulated by tissue removal through factors such as decreased shading of photosynthetic tissue, and activation and increased flow of photosynthates, water, and nutrients to meristematic tissue (Noy-Meir 1993). The grazing optimization hypothesis has

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Research was funded by the Utah Division of Wildlife Resources and Brigham Young University Professional Development Funds.

Manuscript accepted 13 Feb. 03.

probably been over applied (Briske and Heithsmidt 1991), and certainly misinterpreted by those who declare it false using the damage of heavy grazing as evidence (Patten 1993). However, compensation for tissue loss has been well established (Briske 1993). Compensatory growth varies among species and even populations (Painter et al. 1989), and with resource availability for a given species (Williamson et al. 1989, Wandera et al. 1992, Briske 1993). True mountain mahogany tolerates simulated browsing when resources are highly available because of its ability to initiate long-shoot growth from available buds (Wandera et al. 1992). However, ability of true mountain mahogany and other shrubs to compensate for herbivory should be tested under field conditions of actual herbivory and resource availability to best recommend utilization and management guidelines (Wandera et al. 1992, Briske 1993, Noy-Meir 1993, Trlica and Rittenhouse 1993). The purpose of this study was to measure twig and reproductive responses of browsed and unbrowsed true mountain mahogany under field conditions to provide guidelines for its use and management.

Methods

Twig demography was studied on unbrowsed shrubs inside exclosures and browsed shrubs outside at 1 site in the Wasatch Mountains (N 39° 45' 111° 48.8') and at 4 sites on the North Slope of the Uinta Mountains, Utah (N 40° 58' W 110° 4.5–14.5'). Vegetation, soils, and other characteristics of these sites have been described by Turley et al. (2003). Precipitation and temperature data for Gardner Canyon in the Wasatch Mountains were from the Nephi, Utah weather station at 1,520 m elevation located southwest (< 8 km) of the site (NOAA 1995–1999). Precipitation data for the North Slope of the Uinta Mountains were from the Lonetree weather station (NOAA 1995–1999). Lonetree is located about 16 km north of the 4 sites with an elevation of 2,280 m. At Gardner Canyon, 10 mature true mountain mahogany shrubs in the exclosure and 10 in the open area were randomly chosen for branch diagramming (Roundy and Ruyle 1989). Long shoot growth was measured on 3 branches and short shoot growth was measured on 1 branch on each shrub. Short shoots were distinguished from long shoots by their lack of internode elongation for previous years' wood. Ultimately, 30 long-shoot and 9 short-shoot branches were diagrammed in the exclosure, and 29 long-shoot and 12 short-shoot branches were diagrammed in the open area. At the 4 North Slope sites, 3 branch diagrams of long shoots were drawn on each of 3 to 9 randomly chosen shrubs both inside and outside the exclosures. The number of shrubs per site included Gregory Basin inside- 9, outside- 3, Poison Mountain inside- 5, outside- 7, Telephone Hollow inside- 6, outside- 6, Widdop Mountain inside- 5, outside- 5.

Branches were diagrammed to record location and length of annual growth, second-year wood, third-year wood, and location of buds, flowers, and seeds. Branches were drawn freehand to scale on 20 by 28 cm paper. All lengths were measured to the nearest millimeter. Each paper was photocopied, and branches were rediagrammed in the spring after winter browsing, and in the summer or fall after summer growth. Branches were diagrammed for twig growth from 1996 through 1999. At all sites, the number of seeds was recorded on diagrams in the springs of 1997, 1998, and 1999. The number of flowers per branch was recorded in 1997 through 1998 at the North Slope sites and in 1997 and 1998 at Gardner Canyon.

Number of branches diagrammed each year that produced annual growth, flowers, seeds, and that were browsed were counted to determine branch activity. Annual growth browsed as a percentage of total annual growth was calculated to give percent utilization (USDA Forest Service 1979). This results in > 100 % utilization when previous years' growth is browsed. To determine branch size, total twig length of individual twigs was summed for each branch diagram. To determine increases in branch size over time, total twig length for a sample date was divided by total twig length from initial branch diagrams and measurements made in summer and fall 1996

Annual growth estimates included annual growth length per branch and annual growth length at the end of the growing season per total twig length at the beginning of the growing season. Annual twig growth per branch was the current annual growth produced by the individual branch divided by the number of current annual twigs produced by that branch. Flower and seed data were analyzed as numbers per branch, and numbers per total twig length. The number of seeds per flower and branch was also calculated.

The ratio of twig length produced in a given year to total twig length was calculated for 1995 through 1998 to determine differences in branch demography between treatments and over time. For example, ratios of 1998, 1997, and 1996 wood over total twig length and 1995 and older wood over total twig length were calculated.

Total precipitation and mean temperature at Gardner Creek were tested for correlation with mean annual twig growth per branch, mean annual twig growth of growing twigs per branch, mean annual growth length per branch, and mean seeds per branch. Annual growth was tested for correlation for the years 1996 through 1999. Seeds per branch were tested for correlation for years 1997 through 1999. Correlation analysis of North Slope sites used years 1996 to 1999, except for seeds per branch, which used years 1997 to 1999.

An ANOVA mixed model approach using SAS (Littell et al. 1996) was used to statistically analyze data from twig diagrams. Fixed effects included browsing compared to no browsing and site. The random effects included shrubs nested within browsing treatment at the Gardner Creek site and shrubs nested within site and browsing treatment at the North Slope sites. Individual branches were nested within shrubs, browsing treatments, and sites. Shrubs were nested within browsing treatment because they were not blocked within treatments and were a random sample of those plants within that treatment. Sites were kept as a fixed variable, in which case inferences should only be made to the communities that were sampled.

Three types of analysis were done. The first was a simple ANOVA, in which browsed and unbrowsed treatments were compared within a single year. All responses were analyzed with this simple ANOVA to compare treatments within years. Ratio of annual wood was only analyzed in this within-year ANOVA.

The second analysis was a repeated measures ANOVA with year as a class variable in which each year is considered independent of all other years. This was used in the case of the responses of annual growth length per branch, annual growth length per total twig length, annual twig growth per branch, annual twig growth of growing twigs per branch, length browsed per branch, flowers per branch, flowers per total twig length, seeds per branch, and seeds per total twig length. Because these response variables may react differently under different climatic conditions from year to year, each year was seen as a class variable and not continuous. All browsing responses for Gardner Canyon were analyzed with year as the only variable. All browsing responses for the North Slope sites were analyzed for site, year, and their interaction, and when site was significant, only year.

The third type of analysis was a repeated measures ANOVA with year as a continuous variable in which each year was considered dependent on the other years. This was used with the variables total twig length per branch, and total twig length of a given year divided by total twig length in 1996. All sites at the North Slope were analyzed together unless site was significant, in which case an ANOVA was done for each site individually and between treatments.

All 3 types of analysis used a backwards elimination in which nonsignificant effects were taken out of the model to achieve greater sensitivity of the tests by estimating the error terms more accurately. Because P-values < 0.25 may show trends, nonsignificant effects were taken out only when the P-value was > 0.25 to be conservative. Random effects were eliminated first and then fixed effects when necessary. A square root transformation was performed on all data prior to analysis.

Results

Twig Growth

Precipitation variables were significantly ($P < 0.05$) positively correlated with various growth variables for browsed shrubs. At Gardner Canyon and Telephone Hollow annual growth per total twig length was correlated with total precipitation ($r^2 = 0.99, 0.96$). At Gardner Canyon annual growth per branch was significantly correlated with June precipitation ($r^2 = 0.99$). At Poison Mountain and Telephone Hollow, annual growth per branch was correlated with total precipitation ($r^2 = 0.99, 0.96$). At Gregory Basin, annual growth per branch was correlated with August precipitation ($r^2 = 0.98$), while at Widdop Mountain annual growth per branch was correlated with June through August precipitation ($r^2 = 0.95$). Only at Widdop Mountain was there a significant positive correlation between annual growth and precipitation for unbrowsed shrubs. At that site, annual growth per branch was significantly correlated with June through August precipitation ($r^2 = 0.96$). Greater total precipitation and higher summer precipitation for the Nephi station in 1998 and for the Lonetree station in 1997 and 1998 (Figs. 1,2, and 3) were associated with greater annual growth for these years.

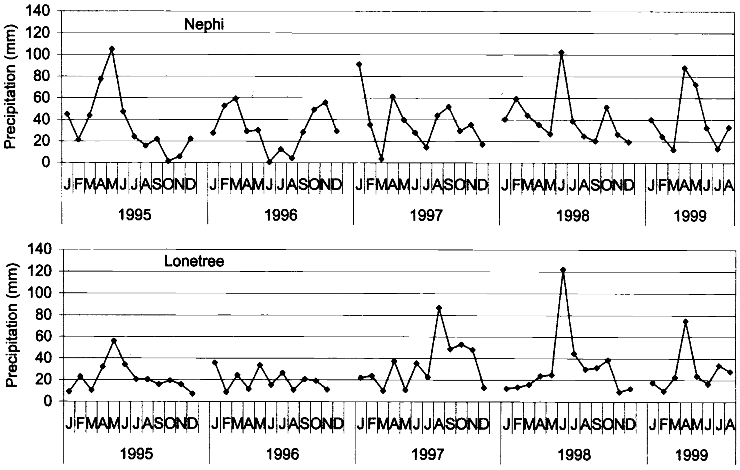

Fig. 1. Monthly precipitation at the Nephi, Utah and Lonetree, Wyo. stations.

Utilization of annual growth averaged 175, 296, and 31% for 1997, 1998, and 1999 at Gardner Creek (Turley et. al 2003). Utilization > 100 % indicates browsing removed previous years' wood. Branches of long shoots at this site with active twig growth averaged 85% for browsed and 55% for unbrowsed shrubs from 1996 through 1999. In contrast, branches of short shoots with twig growth averaged only 33% for browsed and 11% for unbrowsed shrubs. Short shoots at this site grew very little and growth parameters did not vary with browsing treatment or

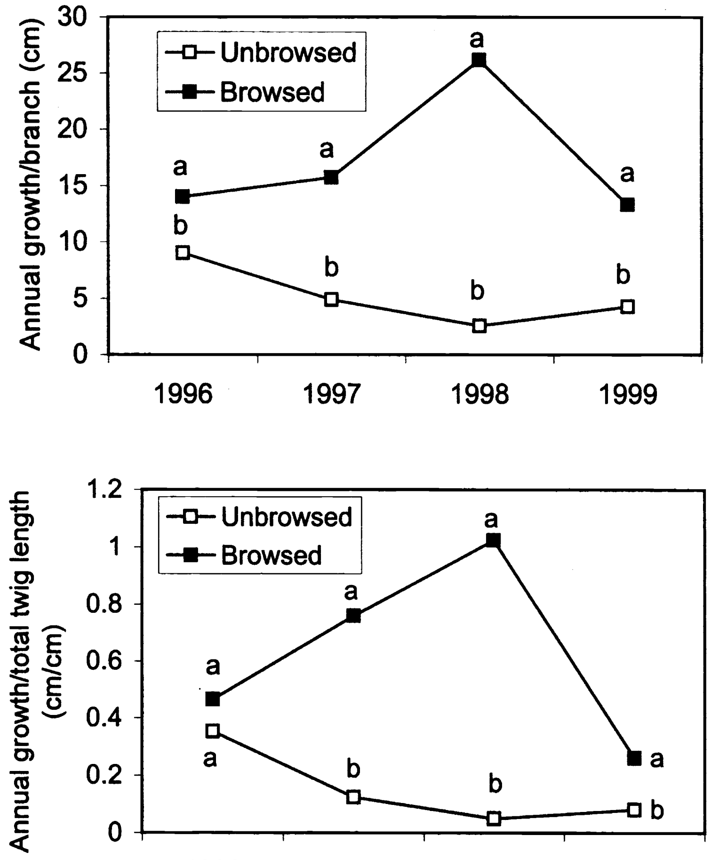

Fig. 2. Annual twig growth per branch (above) and per total twig length (below) for unbrowsed and browsed true mountain mahogany shrubs at Gardner Canyon, Utah Different letters within a year indicate a significant difference ($P < 0.05$).

year. They were easily distinguished from long shoots by lack of internode elongation for previous years' wood. The number of branches with active long shoot growth was high (> 90%) for browsed shrubs following years of high utilization (1997, 1998), but declined (55%) in 1999 after low utilization in the winter of 1998 to 1999. Branches with active long shoot growth declined for unbrowsed shrubs at Gardner Creek from 1996 (90%) to 1999 (33%).

At the North slope, utilization of annual growth for 1997, 1998, and 1999 was 29, 168, and 21% at Gregory Basin; 46, 41, and 50% at Poison Mountain; 302, 306, and 61% at Telephone Hollow; and 149, 83, and 62% at Widdop Mountain (Turley et al. 2003). Branches with active twig growth averaged from 1996 through 1999, for browsed and unbrowsed shrubs were 32 and 31% at Gregory Basin, 59 and 35% at Poison Mountain, 60 and 34% at Telephone Hollow, and 75 and 65% at Widdop Mountain. At all of the North Slope sites and for both browsed and unbrowsed shrubs, the percentage of branches with active growth increased from 1996 through 1997 (42 to 66%), then decreased in 1998 (55%), and 1999 (32%).

The interaction of browsing treatment and year was significant ($P < 0.001$) for growth parameters of long shoots at Gardner Canyon (Figs. 2 and 4). Annual growth of long shoots was greater for browsed than unbrowsed shrubs for all years. However, because of growth removed by browsing, total twig length was similar for browsed and unbrowsed shrubs (Fig. 4). Total twig length for both browsed and unbrowsed shrubs increased over time at Gardner Canyon, however, annual twig growth of unbrowsed shrubs decreased over time (Fig. 2). Annual twig growth of only growing twigs was similar to that depicted for annual growth on a per branch or per total twig length basis in Figure 4.

Growth responses at the North Slope were significant for site, browsing treatment, year, and many of the 2-way interactions of these factors ($P < 0.05$). The 3-way interaction of site, treatment, and year was not significant for any responses. Annual growth length per branch was significantly greater ($P < 0.05$) for browsed than unbrowsed shrubs at Gregory Basin for all years except 1998, and for Telephone Hollow in 1997 and 1998 (Fig. 3). Annual growth length per branch for all other North Slope sites and years did not differ for browsed and unbrowsed shrubs, but annual growth per total twig length was greater for browsed than unbrowsed shrubs for all sites for 1997 through 1999 (Fig. 3). Annual growth of growing twigs only was not greater for browsed than unbrowsed shrubs, but more twigs had active growth on browsed than unbrowsed shrubs. Annual growth per total twig length decreased after 1997 for both browsed and unbrowsed shrubs (Fig. 3). Total twig length per branch was significantly greater for unbrowsed than browsed shrubs at most North Slope sites in most years except 1996 (Fig. 5). Total twig length per 1996 total twig length was greater for unbrowsed than browsed shrubs only at Widdop Mountain. Total twig length per branch increased over time for unbrowsed shrubs at all sites, but more so at Poison and Widdop Mountain, than at Gregory Basin and Telephone Hollow (Fig. 5). Total twig length per branch remained the same over time, or decreased slightly for browsed shrubs.

Ratios of annual wood length to total length grown in a given year measured for diagrammed branches each year provide a demographic picture of twig growth, loss, and replacement through time (Fig. 6). At Gardner Canyon, branches of long shoots of browsed shrubs had increasing ratios of current wood over time, while the opposite was true for unbrowsed shrubs (Fig. 6). Shrubs at Gregory Basin showed the same trends as those at Gardner Canyon in ratio of annual wood. At Poison Mountain and Telephone Hollow there were no signifi-

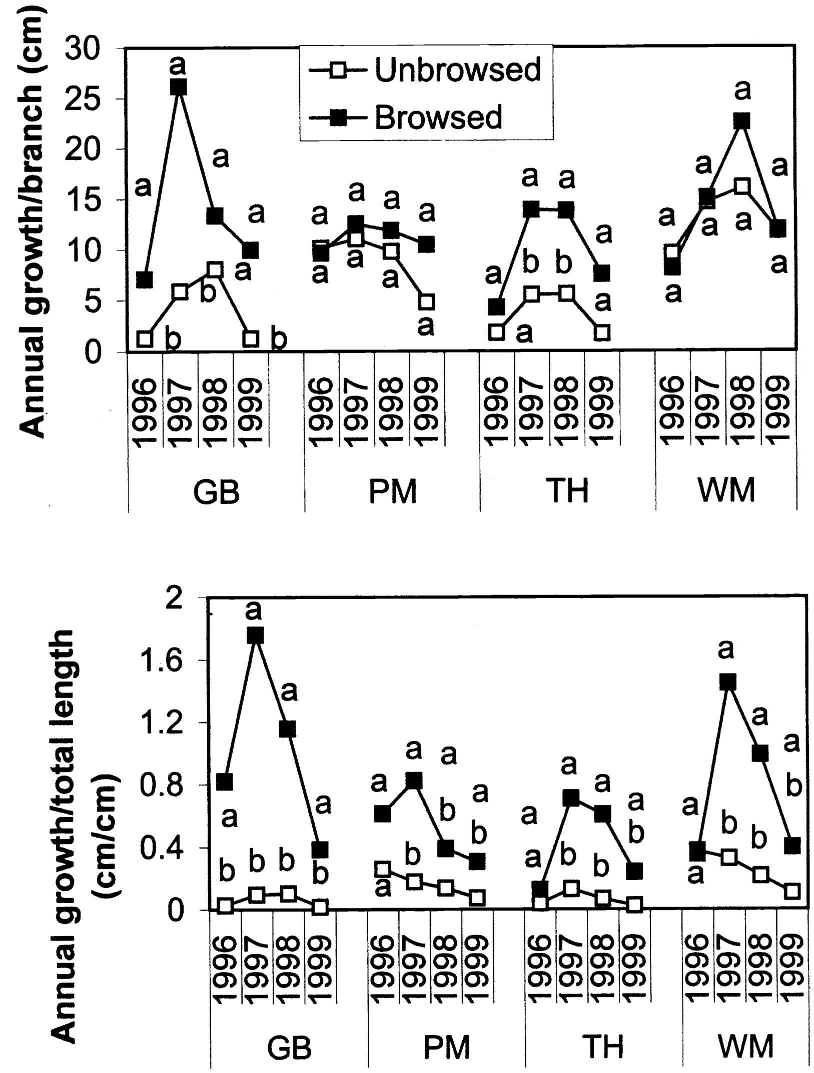

Fig. 3. Annual twig growth per branch (above) and per total twig length (below) for unbrowsed and browsed true mountain mahogany shrubs at 4 sites on the North Slope of the Uinta Mountains, Utah. GB = Gregory Basin, PM = Poison Mountain, TH = Telephone Hollow, WM = Widdop Mountain. Different letters within a site and year indicate a significant difference (P < 0.05).

Table 1. Numbers of seeds and flowers produced by unbrowsed and browsed true mountain mahogany shrubs at 5 sites in Utah.

Site	Variable	1997		1998		1999	
		Unbrowsed	Browsed	Unbrowsed	Browsed	Unbrowsed	Browsed
Gardner Canyon		(No.)					

Long shoots	Flowers /branch	–	–	34.9a	13.4b	1.2a	1.8a
	Flowers/total twig length	–	–	1.0a	0.6b	0.0a	0.0a
	Seeds/branch	10.6a	5.7b	20.7a	10.6b	0.0a	0.0a
	Seeds/total twig length	0.3a	0.1b	0.6a	0.4a	0.0a	0.0a
Short shoots	Flowers /branch	–	–	31.2a	10.1b	1.6a	0.2a
	Flowers/total twig length	–	–	0.5a	0.2a	0.0a	0.0a
	Seeds/branch	18.0a	4.9b	16.0a	8.4a	0.0a	0.0a
	Seeds/total twig length	0.7a	0.1b	0.2a	0.2a	0.0a	0.0a
North Slope Unitas							
Gregory Basin	Flowers/branch	11.2a	2.0a	43.0a	5.2a	7.0a	0.3b
	Flowers/total twig length	0.2a	0.0b	0.7a	0.5a	0.1a	0.0a
	Seeds/branch	6.6a	0.9b	35.8a	2.4a	3.9a	0.0a
	Seeds/total twig length	0.1a	0.0a	0.5a	0.3a	0.0a	0.0a
	Seeds/flower	0.4a	0.1a	0.6a	0.3a	0.2a	0.0a
Poison Mountain	Flowers/branch	38.9a	0.6b	67.2a	3.1b	41.2a	0.0b
	Flowers/total twig length	0.8a	0.1b	1.1a	0.3b	0.7a	0.0b
	Seeds/branch	25.3a	0.3b	64.7a	1.6b	28.2a	0.0b
	Seeds/total twig length	0.5a	0.0b	1.1a	0.2b	0.5a	0.0b
	Seeds/flower	0.6a	0.1b	1.0a	0.1b	0.6a	0.0b
Telephone Hollow	Flowers/branch	13.5a	0.3b	27.5a	0.7b	5.9a	0.0b
	Flowers/total twig length	0.4a	0.1b	0.6a	0.1b	0.1a	0.0b
	Seeds/branch	8.7a	0.2b	19.1a	0.3b	1.7a	0.0a
	Seeds/total twig length	0.2a	0.0b	0.4a	0.0b	0.0a	0.0a
	Seeds/flower	0.5a	0.1b	0.6a	0.1b	0.2a	0.0b
Widdop Mountain	Flowers/branch	2.5a	0.3b	23.9a	5.3b	1.0a	0.0a
	Flowers/total twig length	0.1a	0.0a	0.3a	0.2a	0.0a	0.0a
	Seeds/branch	0.9a	0.3a	12.7a	2.7b	0.2a	0.0a
	Seeds/total twig length	0.0a	0.0a	0.2a	0.1b	0.0a	0.0a
	Seeds/flower	0.1a	0.0a	0.4a	0.1b	0.0a	0.0a

[ab]means for unbrowsed and browsed shrubs within a year with a different letter are significantly ($P< 0.05$) different by ANOVA.

cant differences between unbrowsed and browsed shrubs over time except in 1999, when 1998 and 1999 growth made up a greater proportion of total length for browsed than unbrowsed shrubs. Branches of browsed shrubs at Telephone Hollow had significantly more 1995 wood than branches of unbrowsed shrubs in 1997. Branches of unbrowsed and browsed shrubs at Widdop Mountain did not differ significantly in ratios of annual wood over time except that browsed shrubs had significantly lower ratios of 1996 wood after 1997 than unbrowsed shrubs. Ratio data show how newer growth increasingly replaced older wood and wood lost to browsing.

Flower and Seed Production

At Gardner Creek, the number of seeds per branch was significantly ($P < 0.05$) negatively correlated with mean air temperature in June for both unbrowsed ($r^2 = 0.99$) and browsed ($r^2 = 0.99$) shrubs. Although no correlations of reproductive responses with precipitation variables were significant, greater winter-spring precipitation in 1997–1998 was associated with much greater seed production that spring than in the springs of 1997 or 1999 when winter-spring precipitation was less. No simple positive or negative correlations were found between branches that produced flowers and seeds and branches that produced growth overall or within treatments or years at Gardner Canyon.

At the North Slope, the number of seeds per branch was significantly positively correlated with June precipitation for unbrowsed shrubs at all sites ($r^2 = 0.94$–0.99) and for browsed shrubs for all sites but Telephone Hollow ($r^2 = 0.96$–0.99). For all North Slope sites, seed production was highest in 1998, when June precipitation was highest, and lowest in 1999 when June precipitation was least for years that seed production was measured (Fig. 1, Table 1).

At Gardner Canyon for long shoots, the main and interaction effects of year and browsing were significant ($P < 0.05$) for number of flowers per branch, and number of seeds per branch and per total twig length. For short shoots at Gardner Creek, browsing treatment and year were significant ($P < 0.05$) for the number of seeds per branch and year was significant for the number of seeds per total twig length. Both long and short shoots produced similar amounts of flowers and seeds (Table 1). During the 2 years of highest seed production (1997, 1998), long shoots on unbrowsed shrubs produced almost twice as many seeds per branch as those on browsed shrubs (Table 1). Short shoots on unbrowsed shrubs produced over twice as many seeds per branch in 1997 and flowers per branch in 1998 as those on browsed shrubs. Ratios of seeds per flower for long shoots and short shoots on

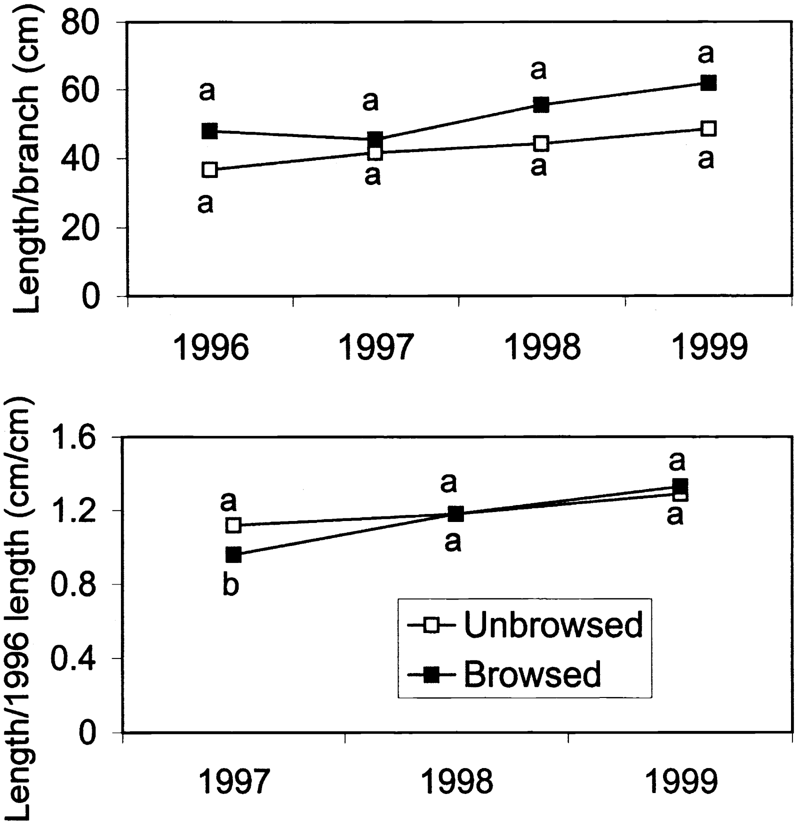

Fig. 4. Total twig length per branch (above) and per total twig length in 1996 (below) for unbrowsed and browsed true mountain mahogany shrubs at Gardner Canyon, Utah. Different letters within a year indicate a significant difference ($P < 0.05$).

unbrowsed shrubs (0.52, 0.41), and on browsed shrubs (0.57, 0.56) did not significantly ($P > 0.05$) differ during the only year measured (1998), which was also the year of highest seed production.

For the North Slope, the effects of site, year, browsing, and the 2-way interactions of browsing with year and with site were significant ($P < 0.05$) for number of flowers per branch, number of seeds per branch, and the number of seeds per flower. The effects of site, year, and the 2-way interactions of browsing with site and year were significant ($P < 0.05$) for the number of flowers per total twig length and the number of seeds per total twig length. Therefore reproductive responses were analyzed separately for each site. On years and at sites with highest seed production, branches on unbrowsed shrubs produced many more flowers and seeds than those on browsed shrubs (Table 1). The number of flowers per branch was significantly greater for unbrowsed than browsed shrubs for all years at Poison Mountain and Telephone Hollow, for 1997 and 1998 at Widdop Mountain, and for 1999 at Gregory Basin. Flowers per total twig length were also greater for all years for browsed than unbrowsed shrubs at Poison Mountain and Telephone Hollow and in 1997 at Gregory Basin. No significant differences were found at Widdop Mountain in number of flowers per total twig length.

Seeds per branch were significantly ($P < 0.05$) greater for unbrowsed than browsed shrubs in 1997 at all sites except Widdop Mountain, in 1998 all sites except Gregory Basin, and in 1999 only at Poison Mountain (Table 1). Seeds per total twig length were not significantly different between treatments at the Gregory Basin site. Seeds per total twig length at Poison Mountain and Telephone Hollow were significantly greater for unbrowsed than browsed shrubs for all years except for 1999 at Telephone Hollow. Seed density at Widdop Mountain was significantly greater for browsed than unbrowsed shrubs in 1998 (Table 1).

Seeds per flower were significantly greater for unbrowsed than browsed shrubs at Poison Mountain and Telephone Hollow for all years and for Widdop Mountain in 1998 (Table 1). Shrubs at the Gregory Basin site showed no significant differences in seeds per flower.

Discussion

Utilization, annual growth, and reproductive responses of true mountain mahogany varied among sites within a given year and among years for a given site. Over the 4 years of the study, annual growth of browsed shrubs compensated for twig length lost to herbivory, even when utilization was over 300 %. Over 100 % of annual growth was browsed during the winters of 1996/1997 or 1997/1998 for 2 of the 4 sites at the North Slope and for the Gardner Canyon site. Animals browsed second and third year growth, as well as annual growth on these sites. Twig growth at the North Slope was greatest in 1997 and 1998, and at Gardner Canyon in 1998. After peaking in the winter of 1997/1998, utilization dropped to less than 65% for all sites in the winter of 1998/1999. Greater growth in 1997 and 1998 may have resulted in less utilization in the winter of 1998/1999, even though animal use was high (Turley et al. 2003).

There was no clear relationship between amount of utilization and annual regrowth among browsed shrubs at different sites. For example, utilization at Poison Mountain was 46, 41, and 50%, while that at Telephone Hollow was 302, 306, and 61% for the winters of 1996/1997, 1997/1998, and 1998/1999. Greater annual growth in 1997 and 1998 compensated for lost twig length in both cases, allowing total twig length on browsed shrubs to be maintained or slightly increase over time (Figs. 3 and 5). Annual growth compensated, but did not over-compensate for tissue lost to herbivory. Therefore, dimensions of browsed shrubs stayed the same, and did not increase in size over the study period. However, unbrowsed shrubs at 4 sites were larger than browsed shrubs (Turley et al. 2003). Although twigs on browsed shrubs grew proportionally more than those on unbrowsed shrubs, twig length per branch was greater and increased more over time on unbrowsed than browsed shrubs at the North Slope (Fig. 5). Even though annual growth compensated for length lost to herbivory after heavy utilization, it was not sufficient to allow browsed shrubs to increase in total twig length and equal the size potential of unbrowsed shrubs.

Grazing-tolerant shrubs like true mountain mahogany are able to compensate for tissue lost to herbivory because they have available growing points and allocate resources to them (Wandera et al. 1992). Under natural herbivory and climatic conditions, there appears to be a dynamic

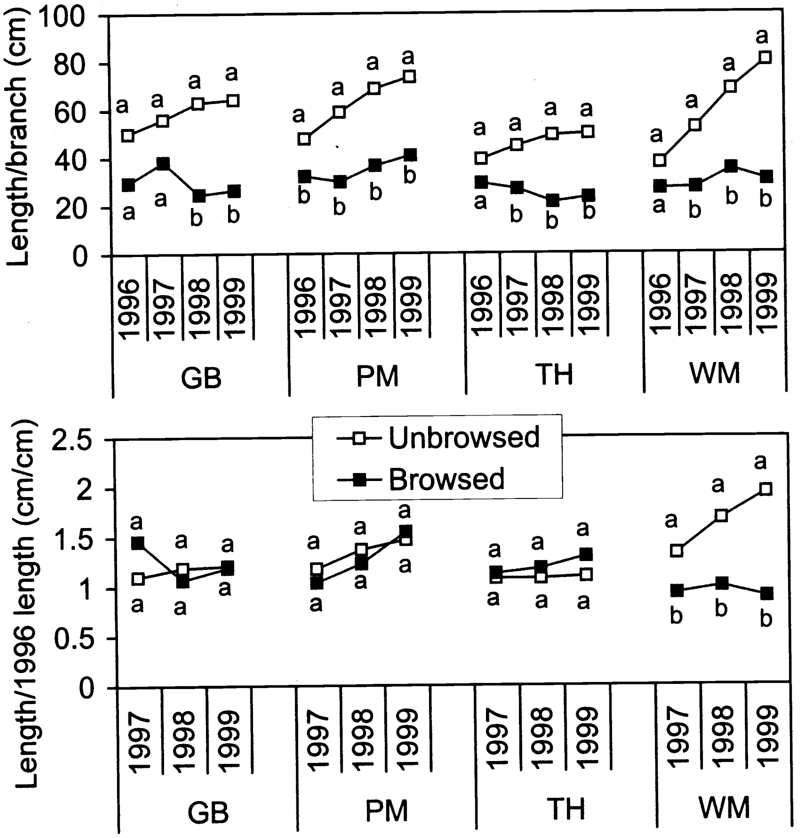

Fig. 5. Total twig length per branch (above) and per total twig length in 1996 (below) for unbrowsed and browsed true mountain mahogany shrubs at 4 sites on the North Slope of the Uinta Mountains, Utah. GB = Gregory Basin, PM = Poison Mountain, TH = Telephone Hollow, WM = Widdop Mountain. Different letters within a site and year indicate a significant difference (P < 0.05).

interaction among animal use, utilization, compensatory annual growth, and resource availability for these shrubs. If resource availability is high during the summer growing season, compensatory growth to replace twig length lost to herbivory during the previous winter will also be high, and total twig length should increase. If animal use or stocking the following winter stays the same as the previous winter, utilization should decrease due to increased biomass from the high compensatory growth. If resource availability is low during the summer growing season, compensatory growth will also be lower, total twig length less, and utilization the following winter would increase under the same animal use. The exact relationship among these variables is not necessarily known for a site. As resource availability and compensatory growth increase for a set of years, total twig length and shrub size could increase from negative to zero or positive where utilization is high (> 100 %), and to that dictated by long-term resource availability or site potential where utilization is lower (< 100 %). Because resource availability cannot be predicted, conservative range management suggests that herd sizes be controlled so that utilization is less than 100 % of previous year's annual growth to maintain shrub size and forage production. Due to the difficulty in accurately measuring annual growth and utilization, a more practical approach may be to monitor cover and size of browsed shrubs and adjust herd size to allow shrubs to reach their productive potential for the site (Turley et al. 2003).

Caution should be used in applying the grazing optimization hypothesis to true mountain mahogany stands, because optimum production may only occur when resource availability is high and shrubs are not reduced in size from past overuse. In this study, growth of browsed shrubs was influenced more by resource availability than utilization during the previous winter. It should also be recognized that grazing has many other effects besides those on individual shrubs of the dominant forage species, and that long-term effects of heavy utilization may have a negative effect, when short term heavy utilization has a stimulatory effect on growth. Long-term heavy utilization (> 100 % annual growth) may reduce carbon fixation and water and nutrient uptake by reducing photosynthetic tissue above ground and root mass below ground. The long-term result may be reduced shrub size and therefore productive potential of the stand, even if shrub density does not decrease (Roundy and Ruyle 1989).

As has been recommended by Holechek et al. (2001) from an extensive review of years of stocking rate research across many vegetation types, moderate stocking and utilization is best when grazing pressure is relatively constant from year to year. The dynamics of big game animal use, resource availability, annual growth, and utilization make it very difficult to manage true mountain mahogany stands for optimum production. Although heavy use (> 100% of annual growth) in 1 or 2 years may not be injurious in the long term, it is best to manage for moderate use on most years and avoid the damage that could occur if utilization is high and resource availability is low.

Browsing had much more of a negative effect on plant reproductive responses than on vegetative responses in this study (Table 1). Unbrowsed shrubs produced many more flowers and seeds than browsed shrubs. Seed and flower numbers on unbrowsed and browsed shrubs were highest in 1998 when either winter-spring or June precipitation was highest. For browsed shrubs, seed and flower numbers varied more among years than among sites with different utilization percentages within a year. Even though utilization was over 300% at Telephone Hollow in the winters of 1996 to 1997 and 1997 to 1998, flower and seed production were much higher in 1997 and 1998 than in 1999 when utilization the previous winter was only 62%.

Because flower production occurs before annual growth, new growth does not provide any reproductive potential for that year in true mountain mahogany shrubs (Walker and Turley 1999). Lack of second year and older wood due to browsing may be partially responsible for significantly less seed production on browsed than unbrowsed plants. However, the fact that unbrowsed shrubs also had greater numbers of flowers and seeds per total twig length suggests that less wood availability may not fully account for lower reproductive responses of browsed than unbrowsed shrubs. Roundy and Ruyle

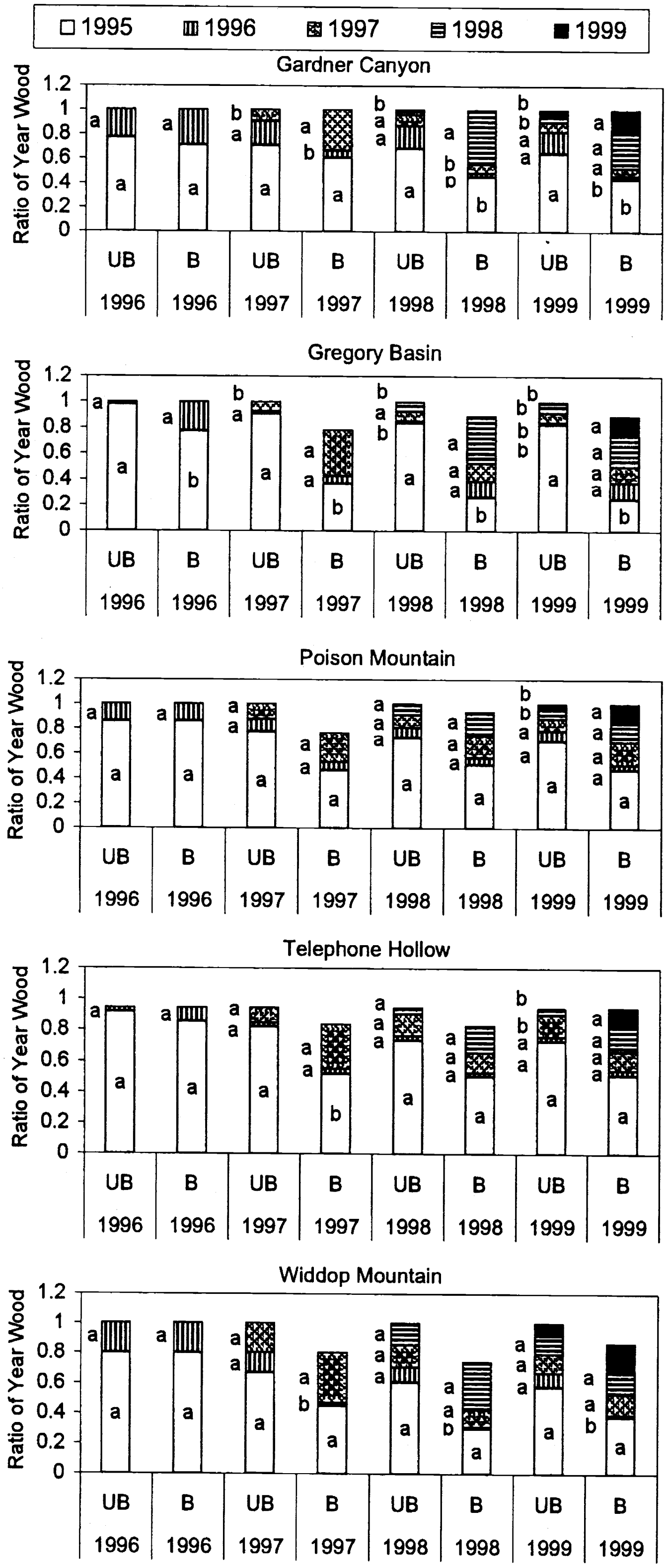

Fig. 6. Ratio of wood length grown during different years (bar patterns) to total length for a given year (x axis) for unbrowsed and browsed true mountain mahogany shrubs at 5 sites in Utah. UB = unbrowsed, B = browsed. Different letters within a site and year indicate a significant difference between unbrowsed and browsed for that year wood as indicated by the same bar pattern ($P < 0.05$).

(1989) also found much fewer flowers and seeds on browsed than unbrowsed jojoba (*Simmondsia chinensis* (Link) Schn.), a grazing tolerant shrub in the Sonoran Desert. Effects of lower flower and seed production due to browsing on long-term seedling establishment and stand renewal for long-lived shrubs are difficult to predict. Turley (2000) found similar densities of seedlings and other size classes of true mountain mahogany inside and outside exclosures at these sites. It is expected that browsed stands will still have sufficient reproduction to maintain the populations of these shrubs over the long term, as long as shrub size is maintained.

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True mountain mahogany community and shrub size responses to browsing

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Abstract

True mountain mahogany (*Cercocarpus montanus* Raf.) provides nutritional winter forage for big game species in the mountain brush zone. To determine browsing effects, animal use, percent vegetation cover, and shrub dimensions were measured inside and outside exclosures up to 7 years old on 4 sites on the North Slope of the Unita Mountains, and at an exclosure > 50 years old in the Wasatch Mountains, Utah. Utilization was measured in an associated twig demography study. Winter big game use increased from 1997 to 1999 at the North Slope. Utilization of annual growth ranged from 21 to over 300%, depending on the site and year and did not necessarily parallel animal use. Greater than 100% utilization of annual growth resulted when previous years' wood was browsed. There was little difference in vegetation cover, species richness, and diversity inside and outside the exclosures, but mountain mahogany had lower cover and smaller size outside than inside the exclosures at 3 North Slope sites. Mahogany cover was similar, but width and breadth of shrubs were smaller outside than inside the > 50-year old exclosure in the Wasatch Mountains. Browsed shrubs maintained their size from 1995 to 1999 at the North Slope, despite over 100 % utilization of annual growth at 3 of the sites in at least 1 year. True mountain mahogany is highly tolerant of winter browsing, and can compensate for > 100% utilization of annual growth by increased growth during wet years. However, continued use of over 100 % of annual growth could reduce cover, shrub size, and forage production during years of lower resource availability. A practical management approach is to monitor cover and size of shrubs inside and outside well-placed exclosures across the winter range over time, and reduce herd numbers as appropriate to allow browsed shrubs to maintain or reach the size of unbrowsed shrubs when their growth has leveled off after a few years of exclusion.

Key Words: utilization, grazing, big game, winter range, herbivory, Utah, mountain brush, exclosures, moose, deer, elk, pronghorn, *Cercocarpus montanus*

Resumen

En la zona montañosa de arbustos el "True mountain mahogany" (*Cercocarpus montanus* Raf.) suministra durante el invierno forraje nutritivo para la fauna silvestre mayor. Para determinar los efectos del ramoneo se midió el uso animal, porcentaje de cobertura y dimensiones de los arbustos dentro y fuera de exclusiones de hasta 7 años de establecidas en 4 sitios de la exposición Norte de las montañas Unita y en una exclusión de mas de 50 años en las montañas Wasatch, en Utah. La utilización se midió en un estudio asociado sobre demografía de ramillas. El uso de esta especie por la fauna silvestre mayor se incremento de 1997 a 1999 en la exposición Norte. La utilización del crecimiento anual varió de 21 a más del 300%, dependiendo del sitio y el año y no necesariamente del uso animal paralelo. La utilización de más del 100% del crecimiento anual resultó cuando la madera del año previo fue ramoneada. Hubo una pequeña diferencia en la cobertura de la vegetación, riqueza de especies y diversidad dentro y fuera de las exclusiones, pero el "Mountain mahogany" tuvo una cobertura más baja y un menor tamaño fuera que dentro de las exclusiones en los tres sitios de la exposición norte. La cobertura de "Mahogany" fue similar, pero lo ancho y alto de los arbustos fue más pequeña fuera que dentro de la exclusión de más de 50 años de establecida en las montañas Wasatch. Los arbustos ramoneados mantuvieron su tamaño del 1995 a 1999 en la exposición norte, a pesar de que su grado de utilización fue más del 100% de su crecimiento anual, lo que ocurrió en los tres sitios al menos durante un año. "True mountain mahogany"es altamente tolerante al ramoneo invernal y puede compensar la utilización de más del 100% del crecimiento anual al incrementar su crecimiento durante los años húmedos. Sin embargo, el uso continuo de más del 100% del crecimiento anual pudieráa reducir la cobertura y tamaño del arbusto y la producción de forraje durante los años de baja disponibilidad de recursos. Una estrategia práctica de manejo es monitorear la cobertura y tamaño de los arbustos dentro y fuera de exclusiones bien ubicadas a lo largo del pastizal de invierno y a través del tiempo y reducir el tamaño del hato en forma adecuada para permitir a los arbustos ramoneados mantener o alcanzar el tamaño de los arbustos sin ramoneo cuando su crecimiento se ha estabilizado después de unos años de exclusión.

True mountain mahogany (*Cercocarpus montanus* Raf.), is one of the most important browse species in the mountain brush zone (Holechek et al. 2001), which is located between the sagebrush (*Artemisia* spp L.)-grasslands and juniper (*Juniperus* spp L.) or aspen (*Populus tremuloides* Michx.)-fir (Abies spp Miller) zones. The high nutritional value of its leaves and young shoots (Brotherson 1992, Rominger et al. 1988), make it a valuable forage for deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), Rocky Mountain bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*), mountain goat

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Research was funded by the Utah Division of Wildlife Resources and Brigham Young University Professional Development Funds.

Manuscript accepted 13 Feb. 03.

(*Oreamnos americanus*), and livestock (USDA Forest Service 1931, Kufeld 1973, Wasser 1982, Rominger et al. 1988). True mountain mahogany shrub communities are found throughout the Great Basin and Rocky Mountains between 1070 and 3050 m (Greenwood and Brotherson 1978). The lower elevational range of this species makes it more available as winter forage than curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt. in T. & G., Davis 1990).

Many shrub species common to the mountain brush zone require moderate browsing to maintain high productivity (Holechek et al. 2001). Lower current year's production of true mountain mahogany within big game exclosures compared to browsed shrubs outside the exclosures in southeastern Wyoming led Waugh (1990) to conclude that some utilization was necessary for optimum production and to avoid stagnation and decadence. Tolerance of browsing depends on the ability of the shrub to replace the biomass removed by herbivory. Biomass replacement depends on the shrub's ability to capture and allocate resources for growth from surviving meristematic tissue (Roundy and Ruyle 1989, Bilbrough and Richards 1993). True mountain mahogany is evidently tolerant of moderate to heavy browsing, recovers within 2 to3 years after heavy use, and has increased growth when browsed (Young 1956, Shepherd 1971, Davis 1990). True mountain mahogany clipped in winter or spring up to 90% of previous year's growth exactly compensated for lost tissue by greater growth of long shoots (Wandera et al. 1992). However, Shepherd (1971) found that when greater than 80% of annual growth was removed by clipping, shrub biomass decreased; and when greater than 100% annual growth was clipped, mahogany shrubs were dead within 10 years. Since ability of shrubs to compensate for tissue removal can be affected by resource availability (Wandera et al. 1992), and actual herbivory may differ from clipping (Trlica and Rittenhouse 1993), effects of herbivory should be measured under field conditions to provide management guidelines.

Heavy winter utilization by big game of true mountain mahogany communities on the North Slope of the Uinta Mountains led to the establishment of big game exclosures in 1992 and 1993 by the USDA Forest Service. Our purpose was to compare animal use, utilization, and plant community and shrub characteristics associated with browsed and unbrowsed true mountain mahogany communities to provide future utilization and management guidelines.

Methods

Study Sites

Study sites included 1 exclosure in the Wasatch Mountains and 4 exclosures on the North Slope of the Unita Mountains (Table 1). The Wasatch Mountain exclosure is in Gardner Creek Canyon, approximately 5 km north of Nephi, Utah, east of I-15 in the foothills, and located inside the Mount Nebo Wilderness Area. The exclosure was established in the 1930s with barbed wire and then reinforced in 1945 with net wire. The plant community is codominated by true mountain mahogany and squawapple (*Peraphyllum ramosissimum* Nutt. in T. & G.). Average annual precipitation is 400 to 560 mm, and mean annual temperature is 5 to 7° C (NOAA 1995–1999).

The Uinta North Slope region is located in Summit County, Utah near the border between Wyoming and Utah. Four exclosures were built from 1992 to 1993 in mountain mahogany dominant communities known for being heavily grazed by elk (Table 1). Serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt.) is associated with mahogany at the Gregory Basin and Telephone Hollow sites, while sagebrush (*Artemisia* L.) is associated or dominant in nearby communities at the Poison and Widdop Mountain sites.

Animal Use

Although pellet count surveys have been used for population surveys and to create an index of habitat use for wildlife (Neff 1968, Collins 1981, Loft and Kie 1981), they have been found to overestimate populations (Babcock 1977). Loft and Kie (1981) found pellet count studies to over- and underestimate habitat use. Despite the

Table 1. Site characteristics of true mountain mahogany communities in Utah where browsing was excluded.

Site	Geology	Soil	Aspect	Location	Slope	Elevation	Years of Exclusion by 1999
					(%)	(m)	
Gardner Canyon	limestone, shale	Bezzant gravelly loam series of loamy-skeletal, mixed, frigid typic calciborolls	North, South	N 39° 45' W 111°48.8'	44	1820	> 50
Gregory Basin	Wasatch formation, landslide deposits	65% of Tinsley family of sandy skeletal, mixed frigid, typic ustorthents; 25% rock outcrop	North	N 40° 58' W 110° 6'	10 – 30	2520	7
Poison Mountain	limy shale, sandstone	Gravelly, heavy silt loams, over gravelly, clay loam subsoil	East	N 40° 58' W 110° 14.5'	20 – 40	2730	7
Telephone Hollow	Mississippian limestone	40% of Marden family deep; 25% of Windhem family moderately deep, loamy-skeletal, carbonatic, typic calciborolls; 20% rocky outcrop	South	N 40° 57.7' W 110° 4.8'	20 – 40	2675	7
Widdop Mountain	same as Telephone Hollow		South	N 40° 57.1' W 110° 4.5'	40 – 60	2645	6

variability, pellet counts are useful in creating an indirect index of ungulate abundance or habitat use (Franzmann and Schwartz 1997, Goodrich et al. 1999). Pellet groups were surveyed at the North Slope of the Uintas in June 1997, 1998, and 1999 to provide an index of ungulate use during winter (1 September to mid-June).

Four pellet group lines were surveyed at each site, starting at the exclosure corners and walking away from the exclosures. Pellet group lines terminated at the end of the mountain mahogany community or at a maximum of 100 m, whichever came first. The width of the line was 1.3 m and all groups found within that area were counted and cleared so that groups would not be counted the following spring.

Animal use was calculated using the number of pellet groups and defecation rates for large ungulates. Winter defecation rates of 13 pellet groups per individual per day were used for both mule deer (Neff 1968), and elk (USDA Forest Service 1974). Babcock's (1977) rate of 17.9 pellet groups per individual per day for the Shiras herd on the North Slope of the Uinta Mountains was used for moose. Because of the difficulty in distinguishing between deer and antelope pellet groups, these groups were combined as 1 estimate.

Utilization

Branches were diagrammed on browsed shrubs at each site in fall after summer growth, and again in spring to determine winter utilization as described by Turley et. al (2003). Three branches were diagrammed on each of 3 to 10 shrubs, depending on the site. Utilization for a winter period was calculated as the percentage of total length removed of total growth during the previous summer for all measured branches for a given shrub. Utilization was greater than 100% when previous years' growth was browsed.

Vegetation Communities

Vegetation was measured in May 1999 for the Gardner Canyon site, and July 1999 for all North Slope, Uinta Mountain sites. Three transect lines were placed inside and outside the exclosure at each site. Transects ranged from 23 to 30 m among sites according to the length of the exclosure. Cover classes were recorded every 1.5 m in a 0.25 m^2 quadrat according to Davis et al. (1995). Cover classes were: 1 = 0.01–1%, 2 = 1.1-5%, 3 = 5.1–25%, 4 = 25.1–50%, 5 = 50.1–75%, 6 = 75.1–95%, 7 = 95.1–100%. The cover classes were converted to the midpoint of the estimate and averaged for each transect line.

Species richness and MacArthur's (1972) diversity index were calculated by vegetation category, site, and treatment using average percent cover data. Ruzicka (1958) similarity indices were calculated from average percent cover of the individual species and the general cover categories of the community. Analysis of variance (ANOVA) was done within sites and between treatments on percent cover by species and life form category.

Shrub Dimensions

At Gardner Canyon, cover transects were also used to describe a 1.3-m wide by 30-m long belt transect. Canopies of all true mountain mahogany shrubs within these transects were measured in 1998 for maximum height, maximum width, and breadth (width perpendicular to maximum width). At the North Slope, 5 shrubs in each cover transect were similarly measured in 1995, 1996, 1997, and 1999. Shrubs measured for size at each site included those for which branches were diagrammed to calculate utilization.

Mixed-model ANOVA approach of the Statistical Analysis System (Littell et al 1996) was used to compare shrub dimensions. Fixed effects included browsed or unbrowsed treatment; random effects included plants within treatment at the Gardner Canyon site. Fixed effects included treatment and site; random effects included plant within treatment and within site for the North Slope sites. Repeated measures ANOVA was also done for North Slope sites with year as a continuous variable. Backwards elimination was done in which nonsignificant effects were taken out of the model to achieve greater sensitivity of the test by estimating the error terms more accurately. P-values < 0.25 may show trends. To be conservative with field estimates, nonsignificant effects were taken out only if the p-value was > 0.25. Random effects were eliminated first, and then fixed effects when necessary. A square root transformation was performed on all data prior to analysis.

Results and Discussion

Animal Use

Total animal use ranged from 8 to 156 animal days/ha (Fig. 1). Although pellet group surveys indicated substantial animal use of the North Slope sites, dominant use by a single species varied with the site. Elk and moose were the primary winter browsers on the North Slope with lesser use by antelope/deer and cattle on some sites. Zornes (1994) found moose and elk pellets common throughout true mountain mahogany communities on the North Slope area. Gregory Basin is part of a cattle allotment, and both Poison Mountain and Telephone Hollow are adjacent to cattle allotments. Cattle graze these areas in the summer and use was most prominent in 1999. Antelope and deer also use these areas in summer and winter and may be browsing mahogany year round. Beale and Smith (1970) found pronghorn to lightly utilize curlleaf mountain mahogany and dwarf mountain mahogany (*Cercocarpus intricatus* Wats.) as winter forage.

Rocky Mountain bighorn sheep have been introduced back to the North Slope of the Uinta Mountains. No pellet groups were found, but difficulty in identifying pellet groups by species may account for this. During this study, no bighorn sheep were seen at the sites, but were seen in the surrounding areas.

Widdop Mountain received greatest animal use while Poison Mountain had least use. Use increased on all sites from the winter of 1996/1997 to that of 1998/1999. Pellet groups were only surveyed at Gardner Canyon after the winter of 1998/1999, but no pellet groups were found. Snowfall in 1999 was light, and elk and deer may not have been forced onto the lower elevation mahogany communities at Gardner Canyon that year.

Utilization

Utilization did not mirror animal use values and was highly variable among sites and years at the North Slope (Fig. 1). Over 100% of annual growth was browsed during the winters of 1996 /1997 or 1997/1998 for 2 of the 4 sites at the North Slope and for the Gardner Canyon site. Animals browsed second and third year growth, as well as annual growth on these sites. Twig growth at the North Slope was greatest in 1997 and 1998, and at Gardner Canyon in 1998 (Turley et al. 2003). After peaking in the winter of 1997/ 1998, utilization dropped to less than 65% for all sites in the winter of 1998/1999. Greater growth in 1997 and 1998 may have resulted in less utilization in the winter of 1998/1999, even though animal use was high (Fig. 1).

Cover and Diversity Responses

Overall, vegetation cover inside and outside the exclosures was similar (Fig. 2). All sites but Gardner Canyon and Gregory Basin had greater cover of true mountain mahogany inside than outside the exclosure. The Gardner Canyon site had few vegetation differences after over 50 years.

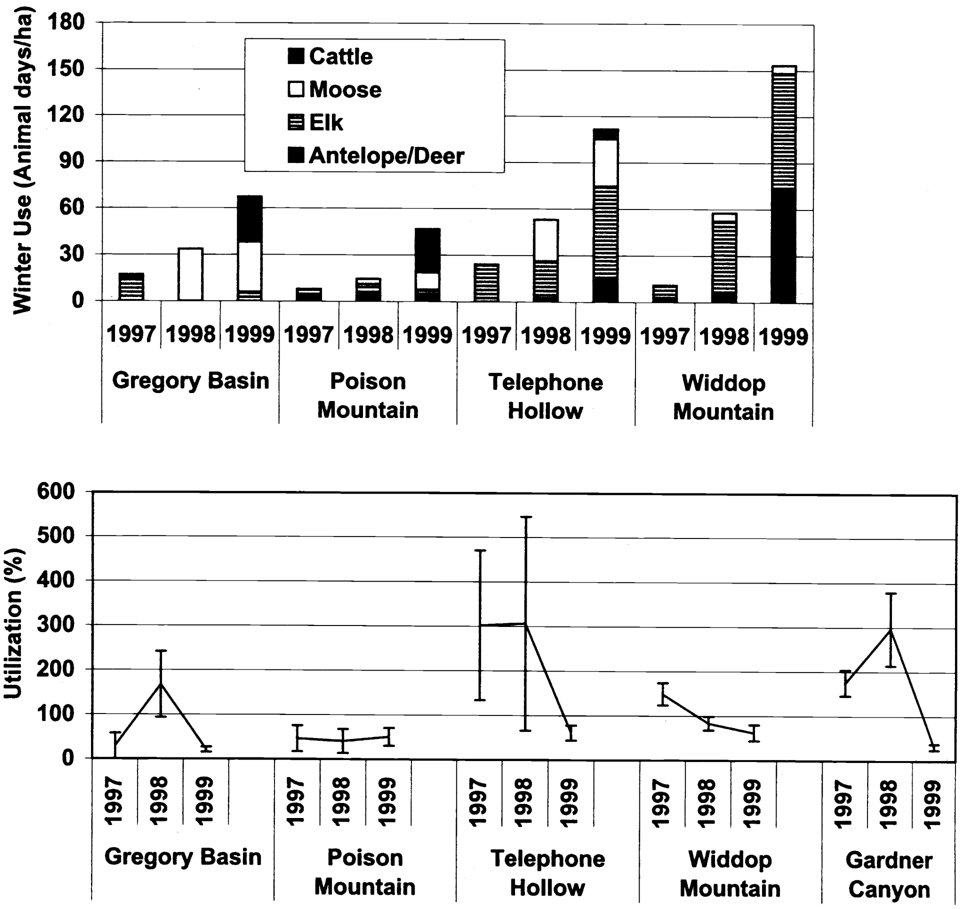

Fig. 1. Winter animal use (above) on 4 true mountain mahogany stands on the North Slope of the Uinta Mountains, Utah, and utilization (below) of mahogany as a percentage of annual growth on those stands and at Gardner Canyon, Wasatch Mountains, Utah.

Squaw apple cover was greater inside (17.8%) than outside (5.7%), while cover of snakeweed (*Guterrizia sarothrae* (Pursh) Britt. and Rusby) was greater outside (6.3%) than inside (0.5%) at Gardner Canyon. Slender buckwheat (*Eriogonum microthecum* Nutt.) had greater cover inside (2.1%) than outside (0.8%) at Gregory Basin. At Telephone Hollow, black sagebrush (*Artemisia nova* Willd.) had 0.4% cover inside and 4% cover outside the exclosure. Shrub species richness and diversity were generally similar inside and outside the exclosures (Table 2). Additional shrub species included serviceberry, big sagebrush, green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook) Nutt.), Oregon grape (*Mahonia repens* (Lindl.) G. Don), snowberry (*Symphoricarpos oreophilus* Gray), and horsebrush (*Tetradymia canescens* DC).

The dominant graminoids at Gregory Basin, and Telephone Hollow were bluebunch wheatgrass (*Elymus spicatus* (Pursh) Gould) and sedges (*Carex* spp. L.), with bluebunch wheatgrass also dominant at Widdop Mountain. Greater cheatgrass (*Bromus tectorum* L.) inside than outside the Gardner Canyon exclosure may be related to spring grazing. The increase of shrub cover and decrease of forb cover inside the Telephone Hollow exclosure may indicate initial community changes. Nixon (1961) also found forbs to decrease with increased tree cover at an exclosure site in the mountain brush zone.

Penstemon spp. Mitch. had greater cover outside (< 0.1%) than inside (0.2%) the exclosure at Poison Mountain, whereas dandelion (*Taraxacum officinale* Weber ex Wiggins) was greater inside (0.6%) than outside (0.1%). Most sites had a wide variety of forbs and forb species richness was similar inside and outside the exclosures (Table 2). An exception was Gardner

Table 2. Species richness and MacArthur diversity index (MacArthur 1972) by site and browsing treatment calculated with percent cover data from inside and outside 5 exclosures in true mountain mahogany communities in Utah in July 1999.

	Species Richness			Diversity Index		
Site and treatment	Graminoids	Forbs	Shrubs	Graminoids	Forbs	Shrubs
Gardner Canyon Unbrowsed	3	6	4	1.72	1.03	2.06
Gardner Canyon Browsed	4	12	4	1.54	1.16	2.40
Gregory Basin Unbrowsed	7	22	9	2.7	9.04	1.90
Gregory Basin Browsed	8	23	8	2.65	7.37	1.55
Poison Mountain Unbrowsed	12	29	7	6.48	6.50	2.40
Poison Mountain Browsed	11	27	7	5.35	6.00	3.68
Telephone Hollow Unbrowsed	7	13	8	2.52	2.83	1.24
Telephone Hollow Browsed	8	19	7	2.36	6.20	2.30
Widdop Mountain Unbrowsed	6	19	9	2.26	5.83	1.42
Widdop Mountain Browsed	7	15	8	2.21	5.23	1.57

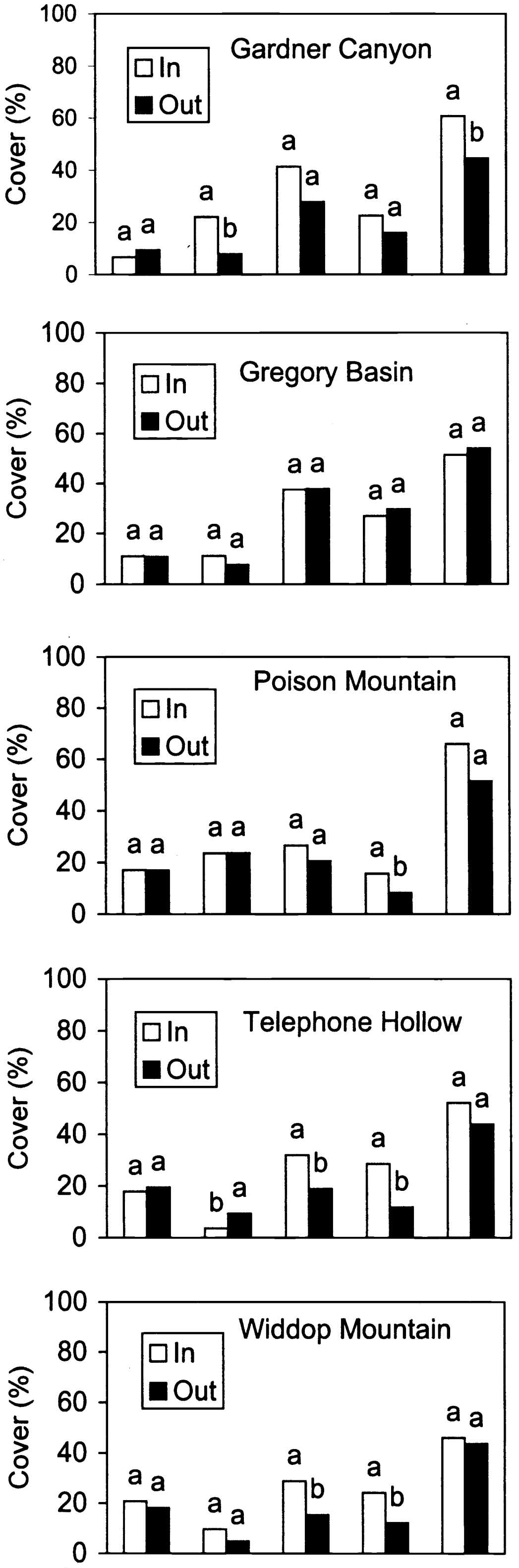

Fig. 2. Vegetation cover inside and outside big game exclosures on 1 true mountain mahogany stand at Garner Canyon, Wasatch Mountains, and at 4 stands on the North Slope of the Uinta Mountains, Utah. Different letters between inside and outside for a vegetation class and site indicate a significant difference ($P < 0.05$). Mah. = true mountain mahogany.

Canyon where lower species richness inside than outside was due to dominance inside by alyssum (*Alyssum alyssoides* (L.) L.) (22.1% cover inside vs. 7.8% outside).

Ruzicka percent similarity indices showed greatest similarity within individual sites and between browsed and unbrowsed communities at the North Slope (Table 3). One exception in the individual species index was that the Telephone Hollow unbrowsed community had a greater similarity to both browsed and unbrowsed communities at Gregory Basin than to the Telephone Hollow browsed community. Cover category indices had higher similarity and less distinction between browsed and unbrowsed communities and sites than indices calculated using individual species. Similarity calculated by the Ruzicka index depends more on dominant than less dominant species (Hajdu 1981). The Gardner Canyon site had a similarity index of 40.7% for individual species and 69.8% for general cover between browsing treatments. Browsed and unbrowsed communities at Gardner Canyon and Telephone Hollow were the least similar for all sites.

Shrub Dimensions

Unbrowsed mahogany shrubs at Gardner Canyon in 1998 had significantly greater crown width and breadth than browsed shrubs (Fig. 3). Although browsing was associated with decreased shrub size, it has not resulted in reduced height compared to unbrowsed shrubs. Browsed shrubs at this site evidently have reached their maximum height or they are out of reach of ungulates.

Shrub dimensions at the North Slope varied with site, browsing treatment, year, and the interaction of site and treatment (Fig. 4). Unbrowsed shrubs at Poison Mountain and Telephone Hollow had significantly greater height, crown width, and crown breadth than browsed shrubs for all years measured, while unbrowsed shrubs at Widdop Mountain were not larger than browsed shrubs until 1999.

Shrubs inside the exclosures at Telephone Hollow increased in size after initial exclusion, but leveled off in growth in subsequent years (Fig. 4). Browsed shrubs at Poison Mountain were smaller than browsed shrubs at all other sites at the North Slope, even though utilization at this site was less than at the other sites. Ferguson (1968) found that bitterbrush shrubs were able to reach mature height in 7 years within an exclosure, and within 11 to 12 years outside the exclosure while heavily browsed shrubs remained smaller.

Table 3. Ruzicka's (1958) percent similarity index calculated on individual species (lower left portion) and general cover categories (upper right portion) of true mountain mahogany communities on 4 browsing exclosures at the North Slope of the Uinta Mountains, Utah, using cover percentages.

	Gregory Basin		Poison Mountain		Telephone Hollow		Widdop Mountain	
	Unbrowsed	Browsed	Unbrowsed	Browsed	Unbrowsed	Browsed	Unbrowsed	Browsed
Gregory Basin								
Unbrowsed		85.43	76.38	81.20	86.80	80.37	83.88	84.06
Browsed	71.37		84.56	75.37	89.81	74.57	72.86	72.11
Poison Mountain								
Unbrowsed	25.02	28.24		68.18	82.92	67.45	66.02	65.48
Browsed	21.12	22.81	53.74		74.40	71.72	74.74	73.20
Telephone Hollow								
Unbrowsed	56.99	63.12	25.28	23.23		76.50	73.75	74.15
Browsed	36.20	34.96	23.61	26.86	49.11		86.72	92.46
Widdop Mountain								
Unbrowsed	43.06	43.31	24.38	17.63	55.30	40.45		93.34
Browsed	31.43	31.97	21.96	21.98	43.64	53.91	57.42	

Shrubs excluded from browsing appear to have recovered to near potential size in just 2 years at Telephone Hollow. Excluded shrubs were still increasing in size after 7 years at Poison Mountain. Evidently browsed shrubs at Gregory Basin are at their potential size because they are the same size as shrubs excluded from browsing for 7 years. At Widdop Mountain, unbrowsed shrubs did not exceed size of browsed shrubs until after the wetter years of 1997 and 1998. These results indicate the interaction between resource availability and response to herbivory or the lack thereof and suggest caution in applying results from 1 time and space to other sites and years (Noy-Meir 1993).

Management Implications

Effects of herbivory should be measured at a range of scales relevant to the scale of management decisions (Brown and Allen 1989, Trlica and Rittenhouse 1993). Differences in browsed true mountain mahogany communities and those unbrowsed for over 50 years in the Wasatch Mountains, and for 6 to 7 years on the North Slope of the Uinta Mountains were not substantial and would be of limited concern to managers, except for the lower cover of true mountain mahogany itself on 3 of 4 sites at the North Slope. Lower cover of browsed than unbrowsed mahogany at Poison Mountain, Telephone Hollow, and Widdop Mountain was associated with smaller browsed than unbrowsed shrubs at these sites. Lower cover and size of browsed shrubs was not necessarily associated with higher utilization of annual growth at these sites during the study period. For example, utilization at Poison Mountain was 46, 41, and 50%, while that at Telephone Hollow was 302, 306, and 61% for the winters of 1996/1997, 1997/1998, and 1998/1999 (Fig. 1). Both utilization and growth varied yearly during the study period and there was no clear relationship between amount of utilization and size among browsed shrubs at different sites. However, that unbrowsed shrubs at 4 sites were larger than browsed shrubs indicates failure of regrowth to exactly compensate for browsed tissue sometime in the past.

Proportional growth of browsed twigs was greater than that of unbrowsed twigs at these sites (Turley et al. 2003). This growth compensation replaced twig length lost to browsing at all sites, regardless of utilization, and allowed browsed shrubs to maintain, but not increase in size. Higher annual precipitation in 1998 at Gardner Canyon and in 1997 and 1998 at the North Slope produced greater twig growth for these years (Turley et al. 2003). This increased twig growth would have resulted in greater biomass production of mountain mahogany throughout the area and may have resulted in decreased utilization at the North Slope in the winter of 1998/1999 even though animal use was still high (Fig. 1). This suggests that years of greater resource availability may allow over- compensation of growth and maintenance of shrub size even when utilization exceeds 100 % on some years. For managers, the risk is that dry or normal years with reduced or average growth coupled with high utilization may result in under compensation and decreased shrub cover, size, forage production, and range carrying capacity.

Holechek et al. (2001) have made a strong case for moderate stocking of livestock such that only 40% of annual growth of grasses is utilized. They cite numerous long term studies to show that such moderate utilization is the best way to maintain and improve rangelands where grasses are a dominant component. Less attention has been given to guidelines for managing big

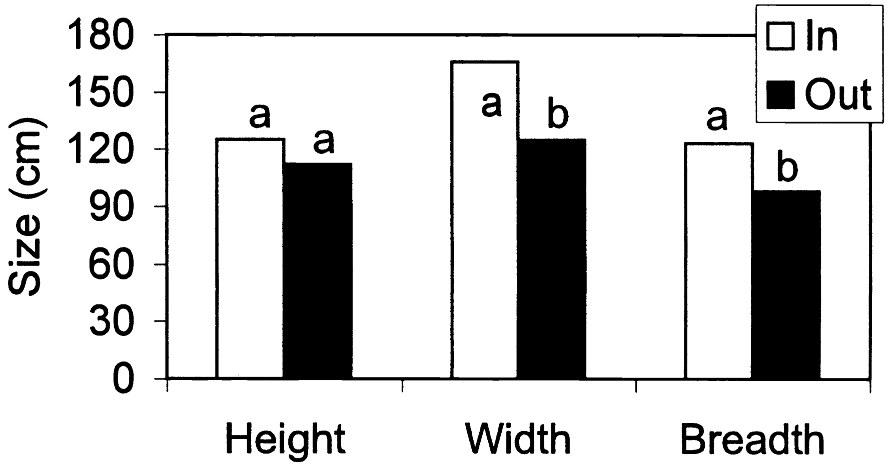

Fig. 3. Dimensions of true mountain mahogany shrubs measured in 1998 inside and outside a > 50 year-old exclosure at Gardner Canyon, Wasatch Mountains, Utah. Different letters for a dimension indicate a significant difference ($P < 0.05$).

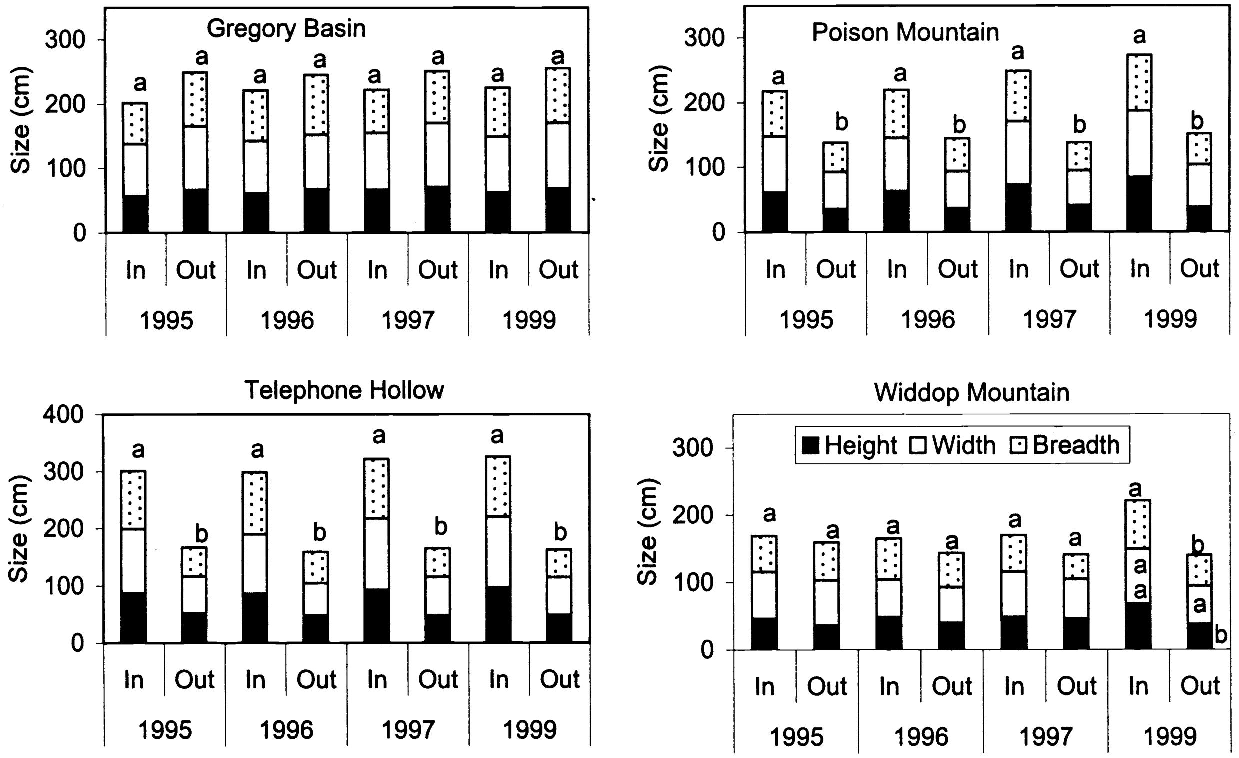

Fig. 4. Dimensions of true mountain mahogany shrubs inside and outside browsing exclosures on 4 sites on the North Slope of the Uinta Mountains, Utah. All dimensions were statistically compared separately. Different letters within a year and site indicate a significant difference (P < 0.05) between inside and outside for all dimensions measured, unless labeled for each dimension.

game on ranges where browsing-tolerant shrubs are the dominant and key forage species. The greater size of true mountain mahogany in this study after just 2 years of exclusion, suggests that on some sites, utilization has been so high that even with years of high resource availability, compensatory growth is not enough to allow shrubs to reach their potential size for the site, thus limiting their potential forage production. Although browsed shrubs did not diminish in size during the study period, their size could have been reduced without the greater precipitation and growth that occurred in 1997 and 1998.

It is difficult to manage big game stocking for specific utilization on certain sites. High animal use in combination with dry or normal years may diminish shrub size by increasing utilization of reduced growth. Subsequent dry or normal years may not allow over-compensation to replace over-utilized growth. Conservative range management would require that grazing-tolerant shrubs such as true mountain mahogany be utilized at less than 100% of annual growth on years of maximum utilization. Monitoring of shrub size and cover is much easier than twig demography measurements to accurately determine utilization, but is also less sensitive to yearly growth and utilization effects. Perhaps the most practical approach, is to monitor cover and size of shrubs inside and outside well-placed exclosures across the winter range over time, and reduce herd numbers as appropriate to allow browsed shrubs to reach the size of unbrowsed shrubs when their growth has leveled off after a few years of exclusion.

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Responses of bahiagrass to nitrogen and defoliation

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Abstract

Pensacola bahiagrass (*Paspalum notatum* Flügge) swards pretreated with fertilizer nitrogen rates of 0 and 66–99 kg N ha^{-1} year^{-1} were exposed to repeated, severe defoliation (i.e., removal of all laminae) of every day (D1), every 2 days (D2), and every 4 days (D4). Responses of the grass were monitored in terms of tiller survival, lamina production and changes in the mass of the stubble-stolon-root system, in an effort to investigate the effects of nitrogen rate and defoliation frequency on defoliation tolerance, to examine differences in survival ability of tillers among tiller age cohorts, and to evaluate contribution of the stubble-stolon-root system to defoliation tolerance. With the progress of defoliation treatments over 12 weeks, the swards degraded with decreasing tiller density, lamina production, and mass of stubble and stolons. Defoliation tolerance in terms of tiller survival was influenced only by defoliation frequency (D1 ≈ D2 < D4), with no significant effect of nitrogen fertilizer rate. There were no differences in survival ability of tillers among age cohorts formed before the defoliation treatments, suggesting that all tillers in bahiagrass were able to share energy and nutrients in connecting stolons under severe defoliation. It was confirmed that stolons play a key role in defoliation tolerance in bahiagrass as the main storage organ supporting aboveground parts, whereas the contribution of roots seems nil.

Key Words: ***Paspalum notatum*, defoliation tolerance, tiller survival, lamina production, stubble-stolon-root system**

Resumen

Praderas de "Bahiagrass" (*Paspalum notatum* Flügge) pretratatdas con dosis de fertilización nitrogenada de 0 y 66-99 kg N ha^{-1} año^{-1} fueron expuestas a defoliación severa (i.e. remoción de toda la lámina) y repetida, cada día (D1), cada 2 días (D2) y cada 4 días (D4). La respuesta del zacate fue monitoreada en términos de sobrevivencia de hijuelos, producción de tejido laminar de la hoja y cambios en la biomasa del sistema rastrojo-estolón-raíz, esto en un esfuerzo por investigar los efectos de la dosis de nitrógeno y la frecuencia de defoliación en la tolerancia a la defoliación, para examinar las diferencias en la habilidad para sobrevivir de los hijuelos entre generaciones de ellos y para evaluar la contribución del sistema rastrojo-estolón-raíz a la tolerancia al a defoliación. Al progresar los tratamientos de defoliación hasta 12 semanas, la pradera se degradó con la disminución de la densidad de hijuelos, la producción de lámina y la masa de estolones y rastrojo. La tolerancia a la defoliación en términos de sobrevivencia de hijuelos fue influenciada solo por la frecuencia de defoliación (D1 ≈ D2 < D4) sin un efecto significativo de la dosis de fertilización. No hubo diferencias en la habilidad de sobrevivencia de los hijuelos entre generaciones de hijuelos formadas antes de los tratamientos de defoliación, sugiriendo que bajo condiciones de defoliación severa todos los hijuelos en "Bahiagrass" fueron capaces de compartir energía y nutrientes entre los estolones conectados. Se confirmó que los estolones juegan un papel clave en la tolerancia a la defoliación de "Bahiagrass" como el órgano principal de almacenamiento sosteniendo las partes aéreas mientras que la contribución de la raíz parece ser nula.

Persistence of grasslands and rangelands is crucial for sustainable agricultural production and/or conservation of the environment (e.g., soil and water), wildlife, and recreational resource. In a grassland community, persistence of grasses is dependent on the ability of plants to maintain a high tiller density and the ability of individual tiller to maintain leaves (laminae) as photosynthetic organs (Hirata and Pakiding 2001, Pakiding and Hirata 2001).

When exposed to continuous severe defoliation, tillers depend greatly on storage organs such as stubble, stolons, rhizomes, and roots for energy supply to maintain themselves and produce leaves. As energy storage in the supporting organs declines, tillers are thought to compete with each other for energy, resulting in earlier death of tillers with lower competitive ability (Zhang and Romo 1995, McKenzie 1997).

Bahiagrass (*Paspalum notatum* Flügge), a sod-forming, warm-season perennial, is widespread in the southern USA and Central and South America (Skerman and Riveros 1989). It is also widely distributed in the low-altitude regions of southwestern Japan. This grass forms a highly persistent sward which tolerates severe defoliation (Beaty et al. 1970, 1977, Stanley et al. 1977, Hirata 1993a, 1993b, Hirata and Ueno 1993). Beaty et al. (1970) reported that bahiagrass performed well even under weekly cuttings at the soil surface level.

However, how bahiagrass behaves under extremely severe defoliation is not fully explored. Only by applying such a condition, we can determine the limit to which each mechanism behind the persistence of bahiagrass successfully works, and understand the overall ability of the grass to tolerate defoliation.

In this study, we imposed repeated, severe defoliation (i.e., removal of all laminae) of different frequencies on bahiagrass swards pretreated with different rates of nitrogen fertilizer, and monitored tiller survival, lamina production, and changes in the mass of the stubble-stolon-root system of bahiagrass. The aims of the study were to investigate the effects of nitrogen rate and defoliation frequency on defoliation tolerance in bahiagrass, to exam-

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Pakiding thanks the Japanese Ministry of Education, Culture, Sports, Science and Technology for financial support during his study in Miyazaki, Japan.

Manuscript accepted 14. Dec. 02.

ine differences in survival ability of tillers among tiller age cohorts, and to evaluate contribution of the stubble-stolon-root system of bahiagrass to defoliation tolerance.

Materials and Methods

Study site and experimental plots and design

The study was conducted on an established sward of bahiagrass at the Faculty of Agriculture, Miyazaki University, Japan (31°50'N, 131°24'E). The meteorological conditions during the study are shown in Fig. 1. In March 1998, 24 plots (30 x 30 cm) were established in the sward. Each plot was isolated from the surrounding area by driving 4 iron plates (30 x 30 cm in area and 3 mm thick) into the soil to a depth of about 26 cm. The 24 plots were grouped into 3 blocks or replications with 8 plots each.

The experiment consisted of 2 stages, i.e., nitrogen treatments from April 1998 to July 2000 and defoliation treatments from August to October 2000. The first stage also included regular tagging of tillers to follow the fate (survival) of individual tiller age cohorts during defoliation treatments. Out of the 8 plots in each block, 2 plots were destructively sampled at the end of nitrogen treatments (beginning of defoliation treatments) to evaluate nitrogen effects on the stubble-stolon-root system. The experimental design at this first stage was an arrangement of 2 nitrogen fertilizer rates, with 3 replications in randomized blocks. Then, the remaining 6 plots in each block were used to evaluate sustained effects of nitrogen and impacts of defoliation on dynamics in tiller density, lamina production, and the stubble-stolon-root system during defoliation treatments. The experimental design at this second stage was a factorial arrangement of 2 nitrogen fertilizer rates x 3 defoliation frequencies, with 3 replications in randomized blocks.

Nitrogen treatments

Two nitrogen treatments (0N and +N) were randomly allocated to the 8 plots in each block (4 plots for each treatment). The +N plots received 8 applications of 33 kg N ha^{-1} over 3 years, i.e., in April, July, and September 1998 and 1999 and April and July 2000 (99 kg N ha^{-1} annually in 1998 and 1999 but only 66 kg N ha^{-1} $year^{-1}$ in 2000). In addition to nitrogen, all plots (including 0N plots) received 27 kg P_2O_5 and 27 kg K_2O ha^{-1} at each application of N. The sources of N, P_2O_5, and K_2O were ammonium sulfate, superphosphate, and potassium sulfate, respectively. During May to October of 1998 and 1999 and May to July of 2000, all plots were cut monthly to a 2-cm height above ground level.

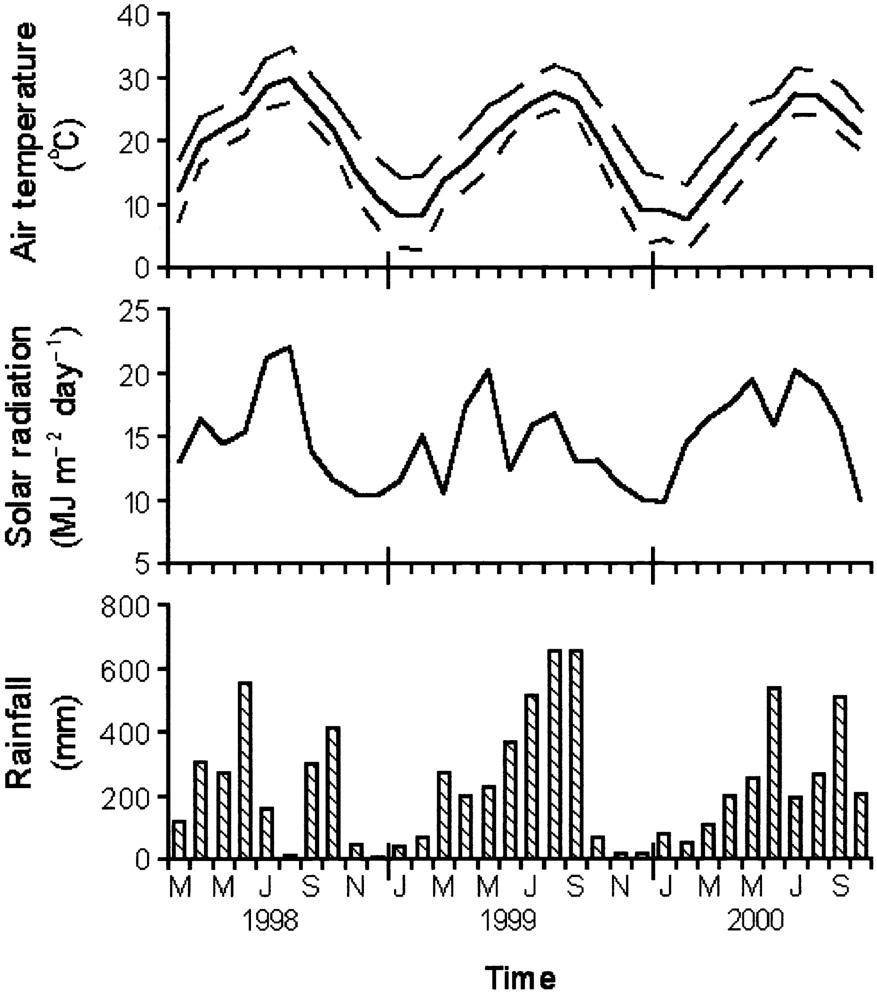

Fig. 1. Monthly means of maximum (-----), mean (——) and minimum (········) daily air temperatures, daily total short-wave solar radiation and monthly totals of rainfall at the Miyazaki Meteorological Station (about 10 km north of the study site) during the study.

Tiller cohort identification

Tillers were regularly tagged during the nitrogen treatments to follow the fate of individual tiller age cohorts during defoliation treatments. On the day of plot establishment (March 1998), a 20 x 20 cm permanent quadrat was established in the center of each plot. All live tillers within the quadrat were tagged with a wire ring (9 mm in diameter) with a colored bead at their base and grouped as the original tillers. This group consisted of tillers with various, unknown ages. Subsequent taggings were conducted at monthly intervals, and rings were removed from dead tillers at the same time. Beads of different colors were used to identify the times of tagging. Tillers were considered as dead when all parts were completely dried. The number of new tillers tagged and the number of rings removed from dead tillers were recorded, from which densities of tillers in different age cohorts at the commencement of defoliation treatments were obtained.

Tillers were classified into the following 11 age cohorts according to the period of their initiation: 1. original tillers formed before March 1998, 2. spring 1998, 3. summer 1998, 4. autumn 1998, 5. winter 1998–1999, 6. spring 1999, 7. summer 1999, 8. autumn 1999, 9. winter 1999–2000, 10. spring 2000, and 11. summer 2000. Spring, summer, autumn, and winter corresponded to March–May, June–August, September–November, and December–February, respectively.

Defoliation treatments and measurements of lamina production, tiller appearance and death

Defoliation treatments commenced in early August 2000 and continued during summer-autumn seasons. At the commencement, all 24 plots were defoliated to a 2-cm height above ground level so that no laminae remained. Three defoliation treatments (D1, D2, and D4) were randomly allocated to 3 of the 0N plots and 3 of the +N plots in each block; leaving a 0N plot and a +N plot in each block for sampling of the pre-treatment mass. D1, D2, and D4 plots were cut every day, every 2 days and every 4 days, respectively, to remove all regrown laminae until all tillers within the central quadrat of any 1 plot were dead. No undefoliated treatment was included because the study aimed to explore behavior of bahiagrass under extremely severe defoliation. Tiller death was judged as described earlier. No fertilizers were applied during the defoliation period.

Lamina yield was measured at each defoliation time, except for the initial cutting. Harvested laminae were oven-dried at 85° C for 72 hours for dry matter determination. Tiller appearance and death were monitored 5 days after the commencement of defoliation treatments and at 8-day intervals thereafter.

Measurements of mass of stubble-stolon-root system

Mass of the stubble-stolon-root system was measured at both the beginning and the end of defoliation treatments. The pre-treatment mass was measured immediately after the initial defoliation from the 0N and +N plots in each block (plots not receiving defoliation treatments) by sampling a 20 x 20 cm to a 25-cm depth below ground surface. The post-treatment mass was measured immediately after the defoliation treatments by sampling to a 25-cm depth using an iron tube 7 cm in diameter.

Samples were washed to remove soil and were then separated into stubble (stems, leaf sheaths, and aboveground dead materials), stolons, roots, and belowground dead materials (dead stolons and roots). Laminae were rarely sampled because of their complete removal by defoliation treatments. Dead stolons and roots were distinguished from live tissues, based on their degree of decay by appearance and touch (color, fragility, and solidity). Tissues under decay were separated and categorized as dead materials. The samples were oven-dried at 85° C for 72 hours for dry matter determination.

Data analyses

The effect of nitrogen treatments on the mass of the stubble-stolon-root system at the commencement of defoliation treatments was evaluated by a paired t-test. The effect of nitrogen (0N and +N) and defoliation (D1, D2, and D4) treatments on tiller density, tiller survival, lamina production and mass of the stubble-stolon-root system was evaluated with ANOVA (block as an independent source of variation) and the means were compared with LSD.

The rate of decrease in tiller density of individual cohort with the progress of defoliation treatments was expressed by a decay constant (b, tillers tiller^{-1} day^{-1}), taking the decrease as an exponential change:

$$N = N_0 \exp(-bt) \qquad (1)$$

where N is the tiller density (tillers m^{-2}), N_0 is a constant (initial tillers m^{-2}), and t is time (day). This equation was fitted separately for data from 2 stages of defoliation treatments (i.e., Weeks 1 to 4 and 5 to 9) because tiller survivorship showed different patterns between these stages. Data after Week 9 were not included in the calculation for decay constants because zero survival (not logarithmically transformable) was common in some treatments. Lamina production rate was expressed as daily yield of laminae which was calculated every 4 days for comparison between D1, D2, and D4 treatments. Percentage or relative change (ΔM_{rel}) in the mass of stubble, stolons, and roots during defoliation treatments was calculated as:

$$\Delta M_{rel} = 100 \times (M_{post} - M_{pre}) / M_{pre} \qquad (2)$$

where M_{pre} and M_{post} are masses (g DM m^{-2}) at the beginning and the end of the treatments, respectively.

Results and Discussion

Sward characteristics at the beginning of defoliation treatments

At the commencement of defoliation treatments (i.e., end of nitrogen treatments), total tiller densities were higher in +N than in 0N (Table 1 and Fig. 2). Within each nitrogen level, total tiller densities did not differ among plots allotted to 3 defoliation regimes ($P > 0.05$). In all treatments, original tillers (formed before the initial tagging in March 1998) and tillers initiated in the following 3 springs showed relatively high densities. In +N treatments, tillers initiated in the 3 summers also showed relatively high densities. Mass of stubble-stolon-root system was between 1,276 and 1,596 g DM m^{-2} (Fig. 3). Stolons accounted for 31 to 36% of total mass (395 to 570 g DM m^{-2}) and belowground dead materials accounted for only 14 to 16% (204 to 225 g DM m^{-2}). +N showed higher mass of stubble and stolons than 0N.

Thus, preceding nitrogen treatments produced swards with different characteristics at the commencement of defoliation treatments. The higher total tiller density and mass of stubble and stolons in +N than in 0N agree with previous observations that an increase in nitrogen fertilizer rate increased tiller density (Pakiding and Hirata 2000) and stolon mass (Hirata 1994) in bahiagrass swards. The relatively high contributions of tillers initiated in spring (0N and +N) and summer (+N) to the total tiller population also agree with previous observations that tiller recruitment in bahiagrass is most active in mid- to late spring or early summer (Pakiding and Hirata 2000, Hirata and Pakiding 2001).

Table 1. Treatment means and ANOVA results (F-value) for tiller densities at the beginning and the end of defoliation treatments and survival rate of tillers.

Nitrogen rate	Defoliation frequency	Tiller density Pre-treatment	Tiller density Post-treatment	Survival
	(days)	--------------------(m^{-2})	--------------------	(%)
0	1	4,600	92	2.0
	2	4,008	108	2.6
	4	4,325	1,442	31.7
+	1	5,242	133	2.6
	2	5,275	58	1.1
	4	6,392	2,417	39.2
Source of variation[1]				
Nitrogen rate (N)		38.9***	1.9	0.2
Defoliation frequency (D)		3.9	26.7***	22.8***
N x D		3.8	1.9	0.3
Block		7.9**	0.3	0.3
LSD(0.05)		820	911	18.0

**: $P \leq 0.01$, ***: $P \leq 0.001$

[1] N x D denotes interaction between N and D. Degrees of freedom are 1 for N, 2 for D, 2 for N x D, 2 for block, and 10 for error.

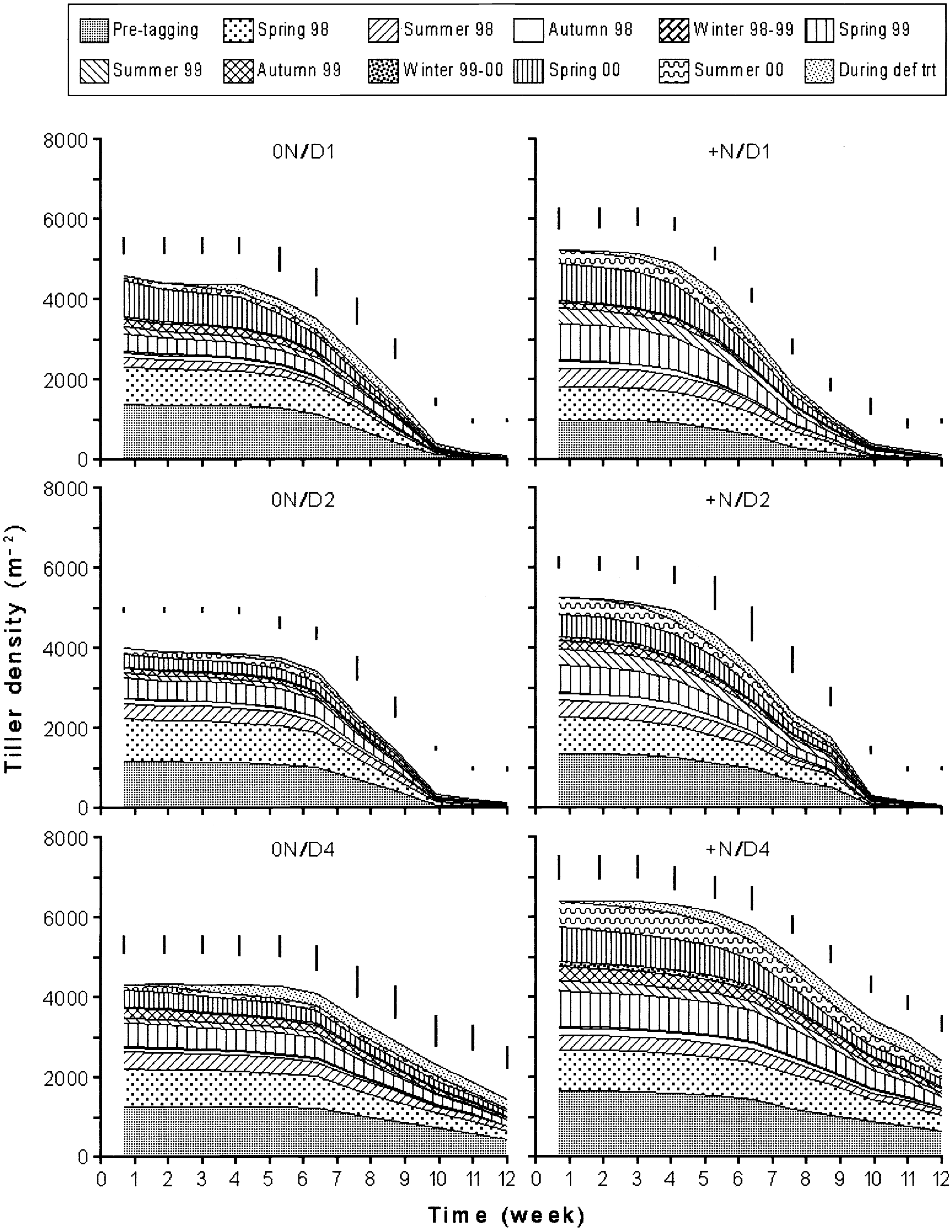

Fig. 2. Changes in density of tillers in different age cohorts after commencement of defoliation treatments over 8-day intervals. Tiller cohorts are stacked in an order of their age (the oldest cohort in the bottom and the youngest cohort on the top): pre-tagging, spring 1998, summer 1998, autumn 1998, winter 1998–1999, spring 1999, summer 1999, autumn 1999, winter 1999–2000, spring 2000, summer 2000, and during defoliation treatments. Vertical bars indicate SE of mean of total tiller density.

Table 2. Decay constant of tiller density (tillers (1,000 tillers)$^{-1}$ day^{-1}) for individual tiller cohorts at 2 stages (Weeks 1 to 4 and 5 to 9) during defoliation treatments.

Weeks	Initiation time of tiller cohorts	0N/D1	0N/D2	0N/D4	+N/D1	+N/D2	+N/D4
1 to 4	Pre-tagging	0.9^{cd}	1.5^{a}	0.3^{a}	2.6^{b}	3.0^{a}	2.0^{a}
	Spring 1998	3.4^{bcd}	2.6^{a}	2.6^{a}	2.9^{b}	5.4^{a}	1.4^{a}
	Summer 1998	5.6^{bc}	2.0^{a}	1.8^{a}	5.8^{b}	5.0^{a}	0.0^{a}
	Autumn 1998	5.9^{bc}	0.0^{a}	7.9^{a}	10.6^{b}	1.8^{a}	3.6^{a}
	Winter 1998–1999	14.5^{a}	0.0^{a}	0.0^{a}	31.5^{a}	-0.1^{a}	0.0^{a}
	Spring 1999	7.1^{b}	2.0^{a}	3.8^{a}	5.2^{b}	7.6^{a}	1.9^{a}
	Summer 1999	4.3^{bcd}	10.2^{a}	3.0^{a}	4.1^{b}	5.7^{a}	2.8^{a}
	Autumn 1999	1.7^{cd}	0.0^{a}	6.1^{a}	4.5^{b}	3.5^{a}	5.2^{a}
	Winter 1999–2000	0.0^{d}	0.0^{a}	0.0^{a}	6.8^{b}	4.0^{a}	0.0^{a}
	Spring 2000	7.1^{b}	5.9^{a}	6.0^{a}	5.7^{b}	2.6^{a}	3.6^{a}
	Summer 2000	0.0^{d}	0.0^{a}	2.4^{a}	3.7^{b}	9.4^{a}	0.5^{a}
5 to 9	Pre-tagging	45.3^{bc}	38.3^{ab}	14.4^{a}	62.8^{a}	33.3^{a}	16.5^{a}
	Spring 1998	47.6^{abc}	53.1^{a}	23.2^{a}	44.4^{a}	36.9^{a}	10.3^{a}
	Summer 1998	34.4^{bcde}	27.4^{ab}	14.9^{a}	63.3^{a}	44.6^{a}	15.6^{a}
	Autumn 1998	38.7^{bcd}	24.7^{ab}	33.7^{a}	86.0^{a}	57.7^{a}	21.5^{a}
	Winter 1998–1999	15.1^{e}	0.0^{b}	51.8^{a}	–[2]	–	0.0^{a}
	Spring 1999	16.4^{de}	42.0^{a}	21.0^{a}	58.8^{a}	48.1^{a}	14.4^{a}
	Summer 1999	55.8^{ab}	48.7^{a}	39.8^{a}	55.8^{a}	27.3^{a}	21.1^{a}
	Autumn 1999	37.0^{bcde}	52.6^{a}	23.6^{a}	61.5^{a}	43.1^{a}	16.8^{a}
	Winter 1999–2000	15.1^{e}	46.4^{a}	14.6^{a}	60.9^{a}	50.6^{a}	25.3^{a}
	Spring 2000	68.2^{a}	45.0^{a}	18.3^{a}	62.1^{a}	45.9^{a}	33.8^{a}
	Summer 2000	30.8^{cde}	27.8^{ab}	2.6^{a}	54.3^{a}	46.9^{a}	19.8^{a}

[1] Values with different alphabetical letters within each treatment at each defoliation stage (weeks) are different at $P \leq 0.05$.
[2] Not calculated because data included zero survival.

Sward dynamics during defoliation treatments

After the commencement of defoliation treatments, tiller densities tended to remain constant for the first 4 to 6 weeks, but sharply declined thereafter (Fig. 2). Almost all tillers were dead after 12 weeks in D1 and D2. The final tiller densities and survival rates of tillers were ranked D1 ≈ D2 < D4, with no significant effect of nitrogen (Table 1). Some new tillers appeared during the defoliation treatment (i.e., the 12th cohort; Fig. 2). Tillers in the 11 age cohorts formed before the defoliation treatments showed similar survivorship and there were usually no significant differences in the decay constants among cohorts within each treatment at each defoliation stage (Table 2).

Lamina production started to decline immediately after the commencement of defoliation treatments and decreased to almost zero after 10 weeks (Fig. 4). Lamina production rate which was higher in +N/D4 than in other treatments throughout the treatment period ($P < 0.05$) was also reflected in the total lamina production (Fig. 5).

By the end of the defoliation treatments, the mass of remaining stolons was as low as 0 to 95 g DM m^{-2} (0 to 6% of total mass) with a trend of D1 ≈ D2 < D4 (Fig. 6). Belowground dead materials, mainly dead stolons, were as high as 507 to 1,136 g DM m^{-2} (46 to 60% of total mass), showing a trend of greater masses in +N/D1 and +N/D2 than other treatments. The mass of stubble and stolons was always reduced by defoliation, but root mass seemed almost unchanged with no consistent trend of increase or decrease (Fig. 7). The percentage loss in stolon mass was greater than that in stubble mass, with the loss tending to be D4 < D1 ≈ D2. By contrast, there were no significant treatment effects on the percentage changes in stubble and root masses.

Plants utilize reserve substances for growth and maintenance when photosynthetic capacity (i.e., leaf area) is limited by defoliation (Briske 1991, Briske and Richards 1994, Heady and Child 1994,

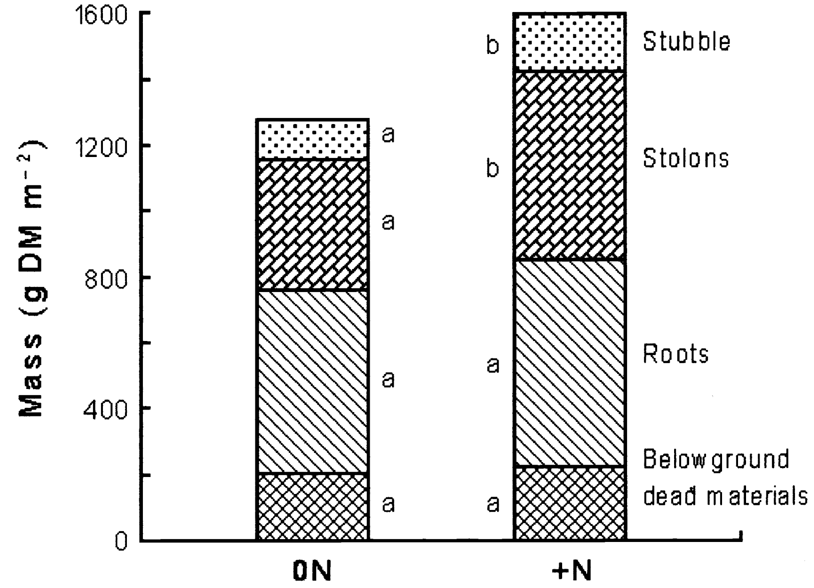

Fig. 3. Mass of stubble-stolon-root system at the start of defoliation treatments. System components are stubble (stems + leaf sheaths + aboveground dead materials), stolons, roots, and belowground dead materials, shown from the top to the bottom. Values with different letters within each component are significantly different at $P \leq 0.05$.

Thornton et al. 2000). Although the current study did not quantify reserves as carbon or nitrogen compounds, the largest biomass losses in stolons within the stubble-stolon-root system (Fig. 7) indicate that bahiagrass coped with the defoliation treatments at the cost of stolons. Thus, the results of this study confirm that stolons play a key role in defoliation tolerance in bahiagrass as the main storage organ supporting aboveground parts (Beaty et al. 1970). On the contrary, the almost unchanged root masses during defoliation treatments (Fig. 7) may reflect little contribution of reserves in root systems to defoliation tolerance in bahiagrass. It has been shown that carbohydrates allocated to root systems in perennial grasses are not capable of being remobilized for subsequent use in aboveground parts following defoliation (Briske 1991, Briske and Richards 1994), even when root mass is reduced by severe defoliation (Heady and Child 1994, Dawson et al. 2000).

The higher tiller survival in D4 than D1 and D2 (Table 1 and Fig. 2) can be largely explained by the fact that tillers in D4 were able to maintain laminae longer than D1 and D2, i.e., D4 tillers were less dependent on remobilized reserve substances. This explanation is supported by the tendency of smaller relative losses in stolon mass in D4 than in D1 and D2 (Fig. 7). In spite of the higher total tiller density and mass of stubble and stolons in +N than in 0N at the commencement of defoliation treatments, tiller survival was not affected by nitrogen rate (0N ≈ +N) (Table 1 and Fig. 2). A possible hypothesis for explaining this phenomenon is that +N tillers consumed more reserves in stolons for lamina production and depleted reserves to the same level as 0N tillers, thus leading to the same degrees of tiller survival in 0N and +N. Hirata (2000) reported that rates of both leaf appearance and extension in bahiagrass increased with increased nitrogen rate. Our hypothesis is supported for D4, as +N/D4 produced more laminae than 0N/D4 (Figs. 4 and 5). However, the hypothesis is not supported for D1 and D2 because lamina production was not significantly influenced by nitrogen rate, though +N tended to show higher production than 0N. Further studies are necessary for fully understanding the mechanisms behind the absence of nitrogen effects on tiller survival in bahiagrass.

Zhang and Romo (1995) and McKenzie (1997), investigating impacts of defoliation on survival of tillers in different age cohorts in northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scribn.) and perennial ryegrass (*Lolium perenne* L.), respectively, observed that the youngest tillers died first when the whole plant was stressed. They attributed the low defoliation-resistance of the youngest tillers to the fact that new tillers are entirely dependent on their parent tillers for energy and nutrient supplies and if parent tillers are defoliated, the resource is diverted for maintaining parent tillers (e.g., lamina elongation) rather than for supporting daughter tillers. However in the current study, the youngest tillers, i.e., produced in summer 2000, did not die most quickly under severe defoliation, usually showing similar survivorship to other cohorts (Table 2). A possible explanation for this inconsistency may be that the youngest tillers of bahiagrass were able to utilize energy and nutrients in stolons without depending greatly on their parent tillers. Bahiagrass has a large mass of stolons (up to 1,200 g DM m^{-2}; Beaty et al. 1970, Hirata and Ueno 1993, Hirata 1994) which act as the main storage organ supporting aboveground growth (Beaty et al. 1970, 1974, Hirata et al. 1990). In the current study, stolons also showed a high biomass of 395 to 570 g DM m^{-2} at the commencement of defoliation treatments (Fig. 3). We thus assume that all tillers shared energy and nutrients in connecting stolons under severe defoliation, though further detailed studies are needed for validating this hypothesis.

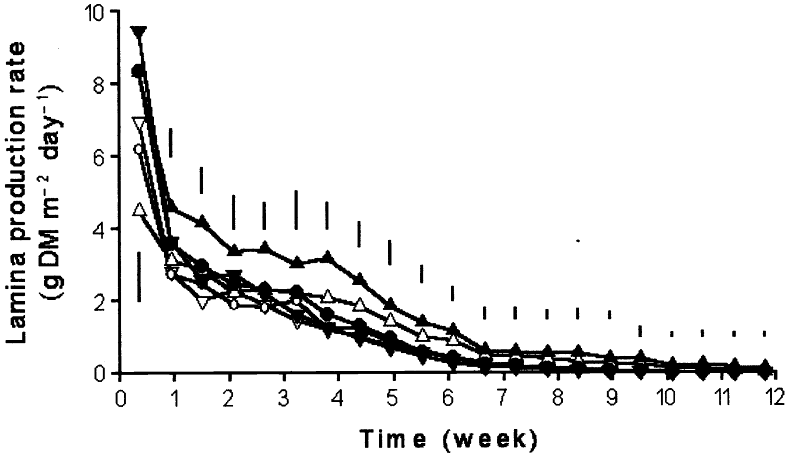

Fig. 4. Changes in lamina production rate after commencement of defoliation treatments. Nitrogen and defoliation treatments are 0N/D1 (∇), 0N/D2 (○), 0N/D4 (Δ), +N/D1 (▼), +N/D2 (●), and +N/D4 (▲). Vertical bars indicate LSD ($P \leq 0.05$).

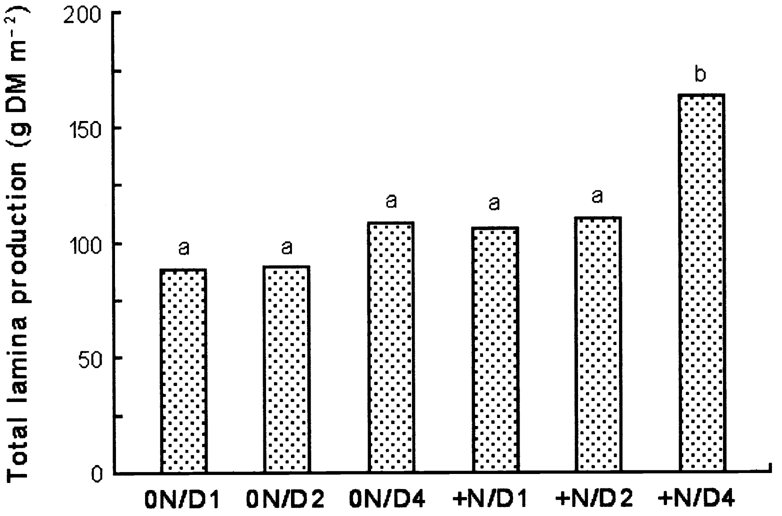

Fig. 5. Total lamina production during defoliation treatments. Values with different letters are significantly different at $P \leq 0.05$.

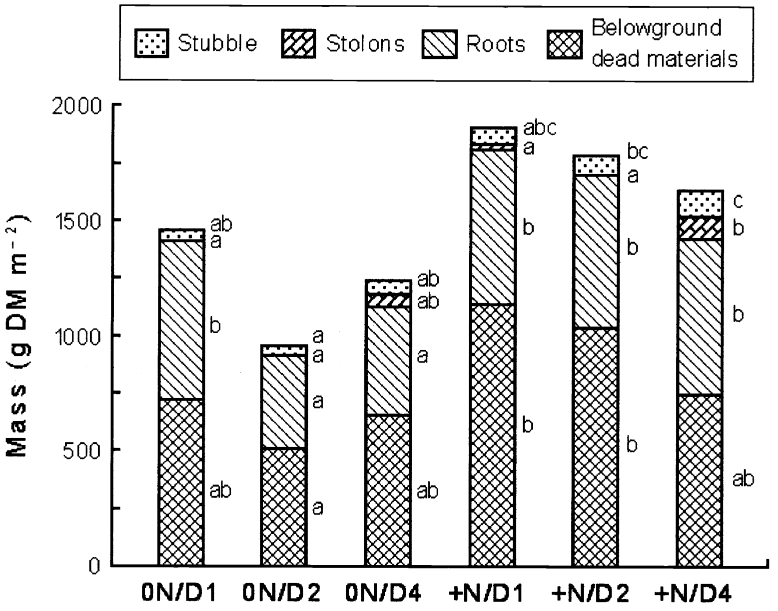

Fig. 6. Mass of stubble-stolon-root system at the end of defoliation treatments. System components are stubble (stems + leaf sheaths + aboveground dead materials), stolons, roots, and belowground dead materials, shown from the top to the bottom. Values with different letters within each component are significantly different at $P \leq 0.05$.

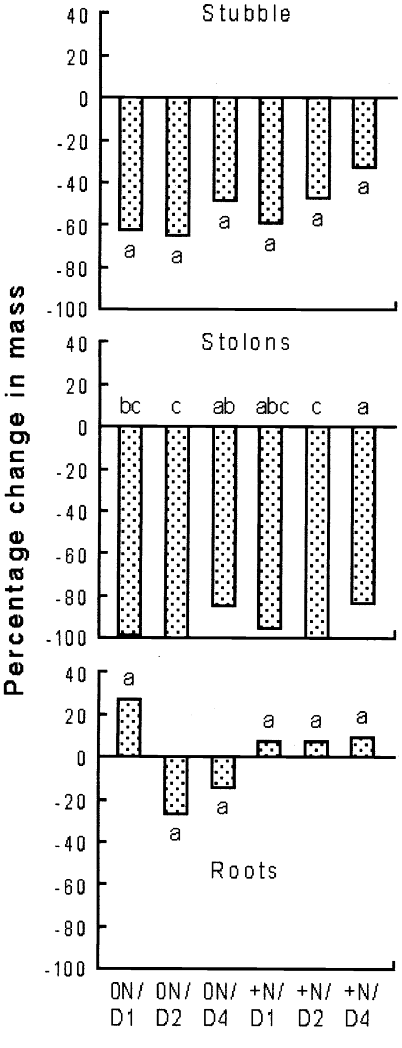

Fig. 7. Percentage changes in the mass of stubble (stems + leaf sheaths + aboveground dead materials), stolons and roots during defoliation treatments. Values with different letters within each component are significantly different at $P \leq 0.05$.

Conclusions

Removing all laminae every 1–4 days degrades bahiagrass swards, with tiller density, lamina production and mass of stubble and stolons being reduced. Survival of tillers and loss of stolon biomass are dependent on defoliation frequency but not on nitrogen fertilizer rate. Unlike some other grasses, survival ability of bahiagrass tillers does not differ among tiller age cohorts, suggesting that all tillers in bahiagrass are able to share energy and nutrients in connecting stolons under severe defoliation. Stolons play a key role in defoliation tolerance in bahiagrass as the main storage organ supporting aboveground parts, whereas the contribution of roots seems nil.

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56: 616-622 November 2003

Big sacaton and endophyte-infected Arizona fescue germination under water stress

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Abstract

Water availability in the germination stage of plants is crucial for seed germination and as a resource for developing seedlings. The effect of osmotic potential on percent germination and time to germination for big sacaton (*Sporobolus wrightii* Munro) and Arizona fescue (*Festuca arizonica* Vasey) was investigated. We predicted that seeds native to semi-arid environments would germinate at osmotic potentials less negative than about –1.5 MPa, the permanent wilting point (PWP) of many agronomic grasses. In addition, the systemic, asexual endophyte *Neotyphodium* is transmitted through the seed in Arizona fescue and is thought to increase germination of its host. Therefore, we also tested for an effect of the endophyte on germination and time to germination of Arizona fescue under varying osmotic potentials. To test for minimum osmotic potential supporting germination, big sacaton and Arizona fescue seeds were placed on acetate membranes in contact with PEG solutions of varying osmotic potentials for 2 weeks. Both grasses germinated at 50% of maximum germination (at soil saturation) at and below the standard PWP (–1.5 Mpa). Big sacaton and Arizona fescue germinated at 64% and 60% at –1.5 MPa, respectively, and Arizona fescue germinated at 35% at –1.8 MPa (70% was the maximum at saturation). The presence of the *Neotyphodium* endophyte did not affect percent or time to germination of Arizona fescue at any of the osmotic potentials tested.

Key Words: ***Festuca arizonica*, *Neotyphodium* endophytes, osmotic potential, permanent wilting point, semi-arid habitats, *Sporobolus wrightii***

Resumen

La disponibilidad de agua durante la etapa de germinación es crucial para que las semillas germinen y como recurso para el desarrollo de las plántulas. Se investigó el efecto del potencial osmótico en el porcentaje y tiempo de germinación del "Big sacaton" (*Sporobolus wrightii* Munro) y "Arizona fescue" (Festuca arizonica Vasey). Predijimos que las semillas de los ambientes semiáridos germinarían a potenciales osmóticos menos negativos de aproximadamente –1.5 Mpa del punto de marchitez permanente (PMP) de la mayoría de pastos utilizados agronómicamente. Además, en el "Arizona fescue" el hongo endófito, sistémico y asexual, *Neotyphodium* se transmite a través de la semilla y se piensa que incrementa la germinación de su hospedero. Por lo tanto, también probamos el efecto del hongo endófito en la germinación y el tiempo de germinación del "Arizona fescue" bajo varios potenciales osmóticos. Para evaluar el potencial osmótico mínimo que sostiene la germinación, el "Big sacaton" y el "Arizona fescue" se colocaron por dos semanas en membranas de acetato en contacto con soluciones de PEG de varios potenciales osmóticos. Ambos zacates germinaron al 50% de la germinación máxima (en suelo saturado) en y abajo del PMP estándar (–1.5 Mpa). A –1.5 MPa el "Big sacaton" y el "Arizona fescue" tuvieron un porcentaje de germinación de 64% y 60% respectivamente, y el "Arizona fescue" germinó un 35% a –1.8 MPa (70% de la saturación máxima). La presencia del hongo endófito Neotyphodium no afectó ni el tiempo ni el porcentaje de geminación del "Arizona fescue" en ninguno de los potenciales osmóticos evaluados.

Establishment and survival of plants in semi-arid regions depends initially on successful germination of seeds under low and ephemeral water conditions. Low osmotic potentials often delay radicle emergence and decrease germination (McGinnies 1960, Qi and Redmann 1993, Brown 1995). Studies that have examined success and timing of germination of semi-arid, native grass species under varying osmotic potentials report that these species have similar osmotic potential requirements as agronomic grass species (Briedé and McKell 1992, Hardegree and Emmerich 1992, Qi and Redmann 1993, Adams 1997). One study, however, found that Idaho fescue (*Festuca idahohensis* Elmer) germinated over a wider range of osmotic potentials with higher germination percentages than non-semi-arid species (Brown 1995), suggesting that native, semi-arid grasses may have adapted to germinate at lower osmotic potentials.

In addition, many pooid grasses are infected with systemic, seed-borne endophytes such as *Neotyphodium* (e.g., Clay 1990). *Neotyphodium* is an asexual fungus that inhabits above-ground tissues of grasses, remains asymptomatic, and often produces alkaloids (Saikkonen et al. 1998, Schulthess and Faeth 1998). These endophytes are vertically-transmitted by hyphae growing into developing seeds (Saikkonen et al. 1998). Systemic endophytes may benefit host grasses in several ways, such as by increasing drought tolerance, herbivore resistance, and seed ger-

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Research was funded in part by a grant from the Howard Hughes Medical Institute through the Undergraduate Biology Enrichment Program, National Science Foundation grants DEB 9727120 and 0128363, and the State of Arizona Game and Fish Department 11PAM Heritage Fund. Authors thank Dr. J. Stutz for providing workspace and the people in S.H.F.'s lab for their help and encouragement.

Manuscript accepted 27 Jan. 03.

mination (Clay 1987, Latch 1993, Elmi and West 1995, Schulthess and Faeth 1998). Arizona fescue (*Festuca arizonica* Vasey) plants are usually infected (60 to 100% of individuals within a population) with the endophyte *Neotyphodium starrii* (Morgan-Jones and Gams) (Schulthess and Faeth 1998), but generally show no increased resistance to herbivores or increased drought resistance at the adult stage (Faeth 2002, Faeth and Bultman 2002, Faeth and Sullivan 2003). Thus, the possible increased germination success of infected seeds may explain the persistence of high levels of infection in natural populations.

We determined the effect of varying osmotic potentials on percentage germination and time to germination of big sacaton (*Sporobolus wrightii* Munro) and Arizona fescue seeds, 2 native grasses, in germination vials with varying osmotic potentials. These grasses were used in this study because they are native, historically and economically important southwestern US forage grasses, and non-commercial seeds of these species were readily available. We also tested whether the endophyte *Neotyphodium starrii* alters percentage germination of Arizona fescue. We predicted that infected (E+) seeds should have higher percent germination than uninfected (E-) seeds.

Methods And Materials

Big Sacaton

Big sacaton is a warm-season (C_4), perennial bunchgrass that grows in dense clumps. It is grazed by cattle and horses in early spring and, has been used historically for making hay (Humphrey 1970). It is found in dry, open, and sandy plains, bottomlands, riverbanks, and alluvial flats from 600- to 1,980-meters elevation. Big sacaton extends from western Texas to California and into central Mexico (Kearney and Peebles 1960, Humphrey 1970, USDA Forest Service 1988). It is drought-resistant, but only after becoming established. Occasional flooding appears necessary for seedling growth (USDA Forest Service 1988). Seeds for this experiment were collected from many individuals in an alluvial bottomland at Gardner Creek, 63 km southeast of Tucson, Ariz., U.S.A. (N 31° 45' W° 110° 36'), in the fall of 1998.

Arizona Fescue

Arizona fescue is a cool-season (C_3), dense, perennial, montane bunchgrass and is important late-season forage for cattle, horses, and sheep (USDA Forest Service 1988). It is native throughout the southwestern United States in open, semi-arid Ponderosa pine forests and dry plains from 1,830 to 3,050 m elevation (Kearney and Peebles 1960, USDA Forest Service 1988). Seeds for this experiment were collected in the summer of 1999 from clones of 4 infected (hereafter, E+) maternal plants in an experiment in progress at the Arboretum of Flagstaff, Ariz., U.S.A (N 35° 10' W 111° 43'). All maternal plants originated from Merritt Draw, about 10 km east of Clint's Well, Ariz. (N 34° 29' W 111° 11'). The endophyte was removed from some clones of each maternal plant using the procedure described in Faeth and Fagan (2002) and Faeth and Sullivan (2003). These clones produced uninfected (hereafter, E-) seeds after 2 seasons of growth in the field.

Design of Germination Vials

Seeds were germinated in vials modeled after Hardegree and Emmerich (1992, Fig. 1). Germination vials were constructed with the following components: a 50-mm diameter by 110-mm high transparent, snap-top plastic vial (Thornton Plastics, Utah, USA); a platform made of extruded acrylic plastic rods (50 mm tall) glued (Ambroid ProWeld®, N.H., USA and Plastruct PlasticWeld®, Calif., USA) to the inside of the vial; and a smaller, transparent plastic, snap-top vial with a diameter of 30 mm. The bottom of the smaller vial was removed to make the vial 26 mm deep and a 23 mm diameter hole was cut into the lid. A cellulose acetate membrane (molecular exclusion weight 3,500), which prevents the transmission of PEG, was placed over the vial's opening and the lid was snapped on over it. The smaller vial (hereafter germination cup) was inverted and placed on the stand inside the larger vial.

Preparation of the Appartus and PEG Solutions

Acetate membranes were soaked in distilled water for about 10 minutes and rinsed 3 times with distilled water. The membranes were snapped onto the germination cups with the lids, and excess water was removed before placement in the larger vials. To equilibrate the membranes with the osmotic solution of polyethylene glycol 8000 (PEG, Baker), about 90 ml of solution was poured into each vial with the germination cups (membrane in contact with the solution) 2 days before the seeds were placed in the germination cups. Therefore, when seeds were placed on the acetate membrane, they were in contact with the osmotic solution. The larger vial's lid was snapped in place to make a closed system (Fig. 1).

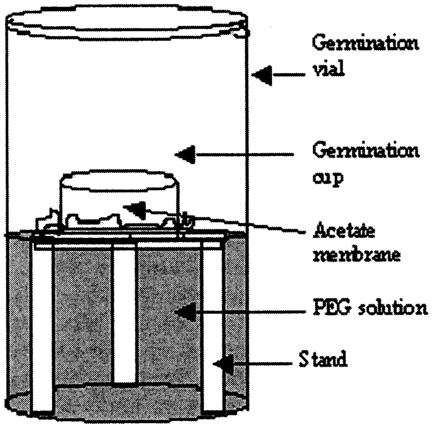

Fig. 1. Schematic of germination vial with germination cup (not drawn to scale). See text for a description of the apparatus.

To confirm the actual osmotic potentials, the various experimental PEG solutions were tested for actual osmotic pressure using a Wescor Vapor Pressure Osmometer at the respective temperatures. Standard curves were derived using 5 KCL standards. Each experimental PEG solution was tested in triplicate. The observed mean MPa of each solution at each temperature was within 0.10 standard deviation (or 0.06 standard error) of the expected, indicating a close agreement of actual MPa of PEG solutions to expected MPa.

Germination Tests

To test the effect of osmotic potential and the endophytic fungus, germination vials with big sacaton seeds were placed randomly in a complete block design and set in a growth chamber. Vials with Arizona fescue seeds were placed randomly in a complete block design on a lab bench. The growth chamber with the sacaton seeds was set to 12 hours of light at 34° C and 12 hours dark at 18° C. The room in which the Arizona fescue seeds were placed was maintained at temperatures between 23 and 26° C.

There were 6 big sacaton treatments with 6 replicates of 50 seeds each. There were 12 Arizona fescue treatments with 6 replicates of 25 seeds each. Although there were only 6 different osmotic solutions used with the Arizona fescue seeds, each infection type (E- or E+) and osmotic solution combination was used. Osmotic solutions were made by mixing PEG with distilled water. The following solutions were made for the big sacaton seeds: 0, –0.3, –0.9, –1.5, –2.25, and –3.0 MPa. The following solutions were made for the Arizona fescue seeds: 0, –0.6, –0.9, –1.2, –1.5, and –1.8 MPa. The PEG/water ratios were calculated based on the following formula by Michel (1983):

$$\psi = 1.30[\mathrm{PEG}]^2T - 137[\mathrm{PEG}]^2 \quad \mathbf{(1)}$$

where ψ is osmotic potential and T is temperature. Big sacaton seeds were checked for germination on days 1, 2, 3, 4, 6, 8, 10, and 15. Observation occurred on days 1, 2, 3, 6, 8, 10, 12, and 14 for the Arizona fescue seeds. Removal of the lids when checking for germination also allowed fresh air into the vials. Seeds were considered germinated and were removed from the vials when a distinct radicle had emerged.

Repeated measures ANOVA (Systat 10.0 GLM procedures) was used to test for differences in percent germination among treatments (between-subjects factor), with time (day of germination) as a within-subjects factor for big sacaton. Similar tests were also used for the Arizona fescue treatments and to test for differences in mean percent germination among treatments and by infection status (between-subject factors) over time (within-subject factor). Difference in cumulative percent germination across all time periods was tested with variation among replicates within osmotic treatments. Percent germination was arcsine transformed (Sokal and Rohlf 1995) for all analyses. Post hoc tests (Tukey HSD, Sokal and Rohlf 1995) were used for pair-wise comparisons among treatments for both plant types and for pair-wise comparisons of percent germination among treatments and infection status over time for Arizona fescue. Repeated measures univariate F tests were also used to compare differences in percent germination between adjacent sampling periods. All assumptions of ANOVA were tested and met.

Results

Big Sacaton

Big sacaton cumulative germination exceeded 50% at osmotic potentials as low as –1.5 MPa (Fig. 2). The greatest germination (98.7%) occurred at 0.0 MPa, declined to 64.2% at –1.5 MPa, and then declined steeply to 8.3% at –2.25 MPa (Fig. 2). Overall, percent cumulative germination showed a treatment effect (Table 1). Pairwise comparisons (Tukey HSD tests) of treatments indicated cumulative germination in all treatments differed from each other (P < 0.01), except mean germination in treatments 0.0 MPa and –0.60 MPa and treatments -2.25 MPa and –3.00 MPa (P > 0.05) (Table 1).

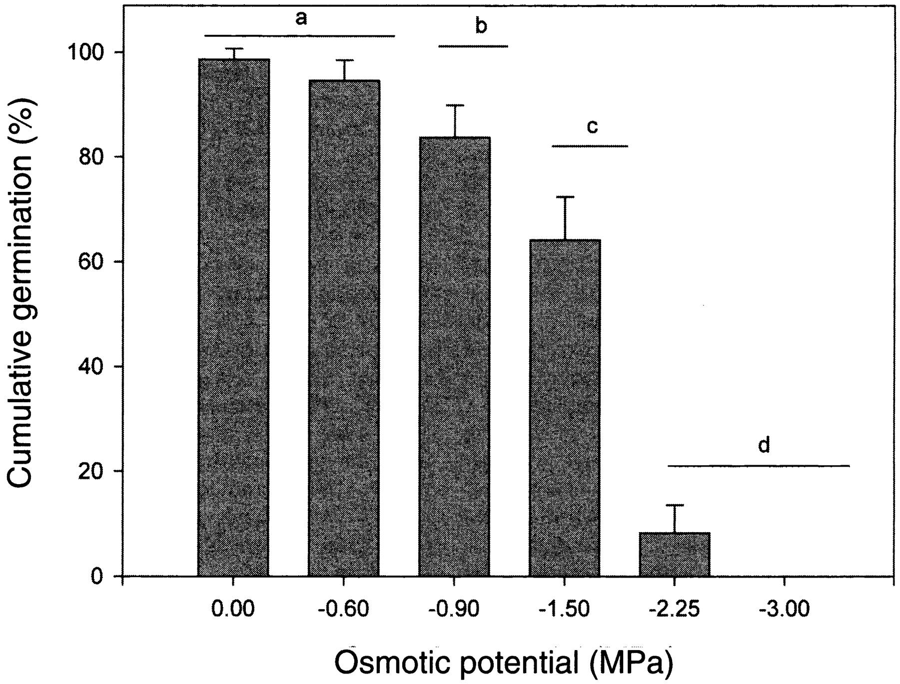

Fig. 2. Mean (± SE) cumulative percent germination of big sacaton at different osmotic potentials. Different letters above bars indicate mean significant differences (P < 0.05, Tukey HSD test).

Percent germination also showed a time effect (Fig. 3, Table 1). Germination among various osmotic potentials also varied differently over time (Fig.. 3, Table 1, time x treatment effect). Generally, seeds in the less negative osmotic potentials germinated earlier than those in more negative osmotic potential treatments (Fig. 3). Germination in the 0.0 MPa and –0.6 MPa treatments peaked on day 2, in the –0.9 MPa treatment on day 3, and in the –1.5 MPa and –2.25 MPa treatments on day 6 and 8, respectively (Fig. 3). No germination occurred in the –3.0 MPa treatment (Fig. 3). Percent germination differed among all adjacent time periods (univariate F tests, P < 0.01), except between days 10 and 15 (P = 0.37).

Arizona Fescue

Cumulative percent germination of Arizona fescue differed among the osmotic potential treatments (Figure 4, Table 2, treatment effect). However, cumulative percent germination remained high (> 60%) as osmotic potentials became more negative and did not decline significantly until –1.5 MPa (Tukey HSD test, P = 0.031). An additional decrease in osmotic potential further reduced cumulative percent germination (Fig. 4, P < 0.001). Germination at all osmotic potential treatments varied with time (Table 2, time effect). Univariate F tests indicated that germination differed among treatments in all adjacent time periods. At more negative osmotic potentials, there was a trend

Table 1. Repeated measure analysis of variance of the effect of osmotic potential (OP) treatments on percent and timing (day) of germination of big sacaton.

Source	Sum of Squares	df	Mean Square	F-ratio	P
Between Subjects					
OP	1690.4	5	338.1	463.2	0.000
Error	21.9	30	0.7		
Within Subjects					
Day	2875.8	7	410.8	69.4	0.000
Day x OP	9726.2	35	277.9	47.0	0.000
Error	1242.6	210	5.9		

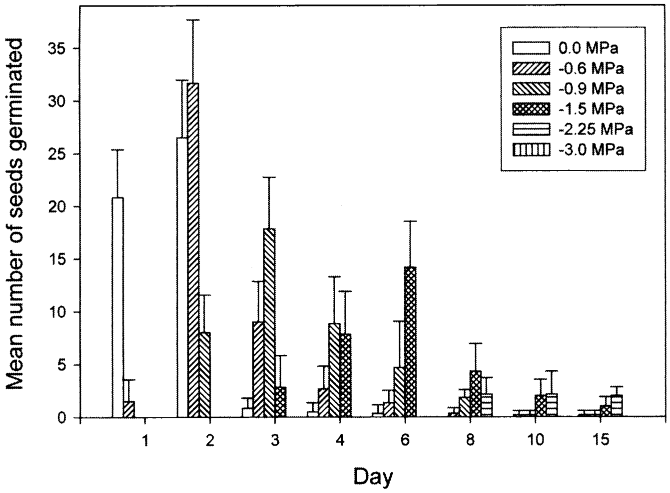

Fig. 3. Mean (± SE) germination success of big sacaton over a 15-day period at different osmotic potentials. Each bar represents the mean (± SE) of 6 replicates of experimental units of 50 seeds.

for delay of germination of Arizona fescue. Germination peaked on day 3 and 6 for the 0.0 MPa treatment, on day 6 for treatments -0.3 MPa and –0.9 MPa, on day 8 for treatments –1.2 MPa and –1.5 MPa, and on day 12 for treatment –1.8 MPa (Fig. 5).

The presence of the endophyte did not affect cumulative percent germination (Fig. 4, Table 2, no endophyte effect) nor did cumulative percent germination of E+ and E- seeds interact differently with changing osmotic potentials (Table 2, no endophyte x treatment interaction). Furthermore, germination of E+ and E- seeds did not differ among treatments over any of the time periods (Fig. 5, univariate F tests, P > 0.24).

Table 2. Repeated measure analysis of variance of the effect of osmotic potential (OP) treatments and infection by Neotyphodium (endophyte) on percent and timing (day) of germination of Arizona fescue.

Source	Sum of Squares	df	Mean Square	F-ratio	P
Between Subjects					
OP	128.4	5	25.7	18.3	0.000
Endophyte	0.3	1	0.3	0.2	0.654
OP x Endophyte	13.4	5	2.7	1.9	0.106
Error	84.2	60	1.4		
Within Subjects					
Day	1199.6	6	199.9	57.2	0.000
Day x OP	1938.6	30	64.6	18.5	0.000
Day x Endophyte	18.9	6	3.1	0.9	0.494
Day x OP x Endophyte	100.9	30	3.4	1.0	0.525
Error	1257.4	360	3.5		

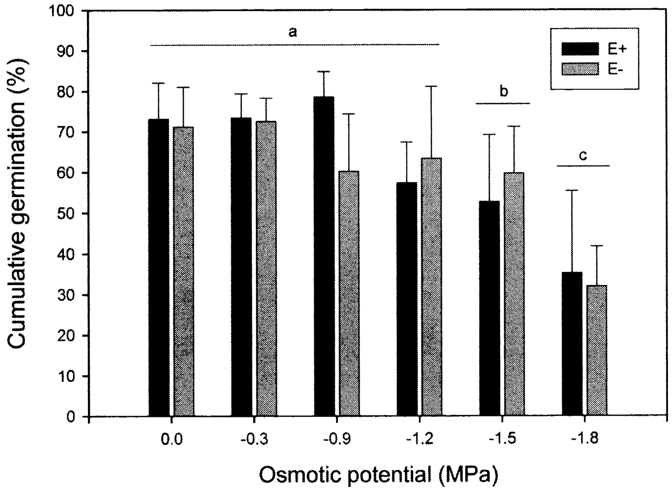

Fig. 4. Mean (± SE) cumulative percent germination of Arizona fescue at different osmotic potentials. Different letters indicate significant differences (P < 0.05, Tukey HSD test). Each bar represents the mean (± SE) of 6 replicates of experimental units of 25 seeds. Dark bars are seeds infected with the *Neotyphodium* endophyte; gray bars are seeds with the Neotyphodium endophyte experimentally removed from the maternal plants.

Discussion and Conclusion

Big Sacaton

Relative germination of big sacaton seeds was greater at more negative MPa values than many other warm-season, semi-arid native grasses. For example, Baskin and Baskin (1998a) reported that weeping lovegrass (*Eragrostis curvula* Schrad.), Lehmann lovegrass (*E. lehmanniana*), tobosa grass (*Hilaria mutica* Buckl.), Johnson grass (*Sorghum halepense* L.), alkali sacaton (*Sporobolus airoides* Torr.), spike dropseed (*S. contractus*), and sand dropseed (*S. cryptandrus* Torr.) declined to less than 50% germination at osmotic potentials more negative than –1.5 MPa. Instead, big sacaton appears to germinate similar to sideoats grama (*Bouteloua curtipendula* Vaughn.), black grama (*B. eriopoda* Torr.), blue grama (*B. gracilis* H. B. K.), and bush muhly (*Muhlenbergia porteri* Scribn.). Germination of these warm season grasses did not decline to 50% or less until osmotic potentials were more negative than –1.5 MPa (Baskin and Baskin 1998a).

The steep decline in percent germination of big sacaton seeds at –2.25 MPa suggests that the critical osmotic potential is between –1.5 and –2.25 MPa. This is contrary to a report by USDA Forest Service (1988) suggesting that big sacaton would not germinate well in low osmotic potentials. Our experiment, however, was conducted in a laboratory using an optimum temperature range, and the seeds were subjected to constant osmotic potentials within each treatment. Thus, our laboratory conditions may not have captured the variability in soil water present in natural

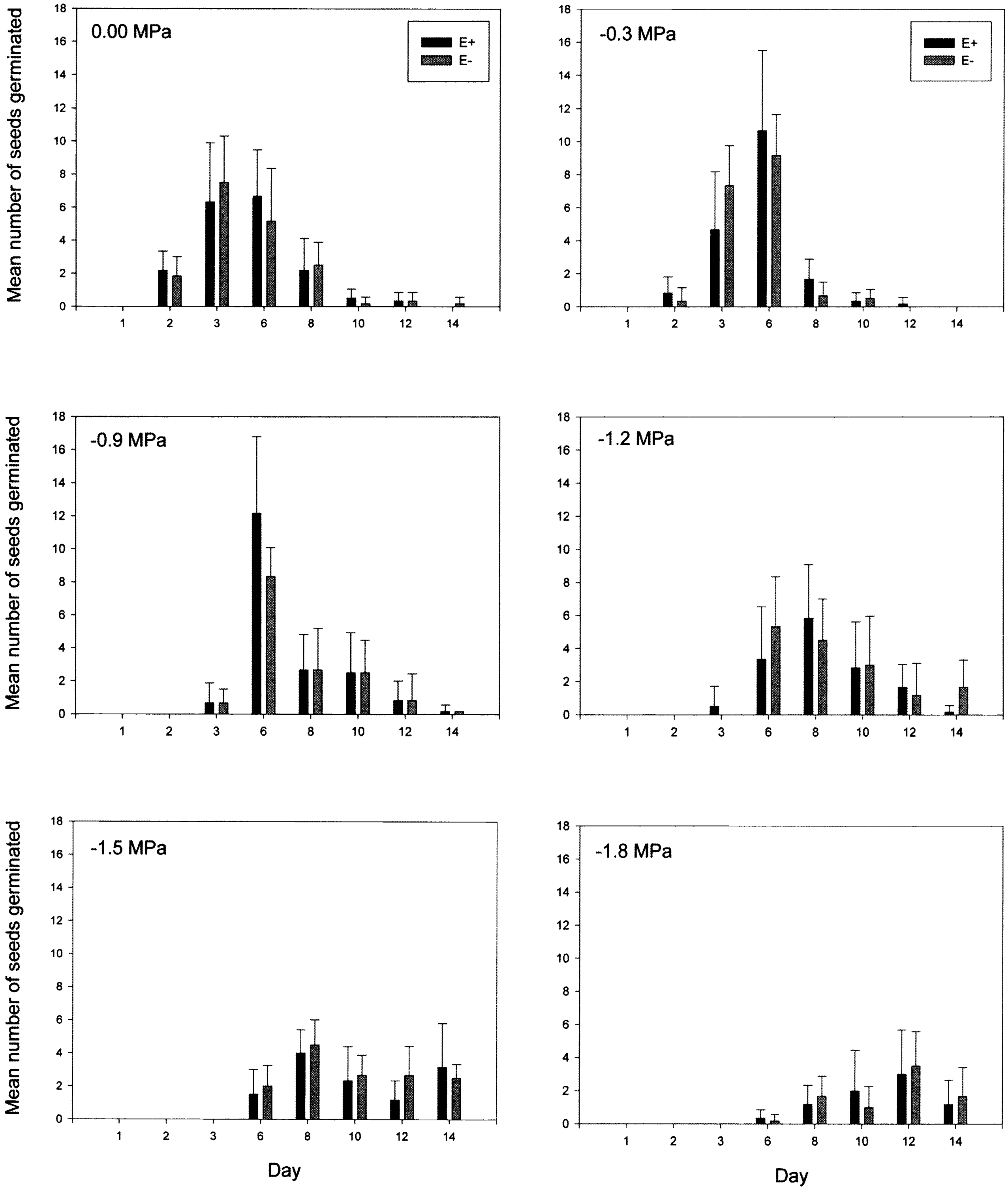

Fig. 5. Mean ± time of Arizona fescue germination over a 14-day period at different osmotic potentials. Mean germination of E+ (infected) seeds did not differ from E- (uninfected) seeds at any osmotic potential or at any time period. Dark bars are seeds infected with the *Neotyphodium* endophyte; gray bars are seeds with the *Neotyphodium* endophyte experimentally removed from the maternal plants.

settings. Further study is necessary to determine if high germination success compared to other semi-arid species and to past studies may have resulted from the artificial conditions of the laboratory, regional adaptation to southern Arizona, or some other factor.

The delay in peak germination at more negative osmotic potentials was expected. Delayed germination at more negative osmotic potentials has been observed for numerous other grasses and plants (McGinnies 1960, Qi and Redmann 1993, Brown 1995). The decreasing magnitude of peak germination paralleled declining germination with more negative osmotic potentials.

Arizona Fescue

Although Arizona fescue is a cool-season C_3 grass that inhabits wetter and cooler areas than big sacaton (Kearney and Peebles 1960, Schulthess and Faeth 1998), total germination did not decline appreciably until –1.5 MPa (Fig. 4). Surprisingly, this is a more negative osmotic potential than that at which big sacaton first showed a significant decline (–0.9 MPa). These results suggest that Arizona fescue germinates over a wide range of osmotic potentials, similar to, and perhaps even more flexible than, a warm-season C_4 grass inhabiting drier regions. Generally, total germination was high compared to germination of other *Festuca* species. For example, Romo et al. (1991) reported germination of plains rough fescue (*Festuca scabrella* Torr.) of about 50% at 25° C and –0.20 MPa. However, this could be an artifact of experimenting in the laboratory, dormancy, or other unknown factors.

Our prediction that infection by the *Neotyphodium* endophyte enhances germination success was not supported. Further, percent germination of E+ and E- seeds did not differ across osmotic potentials. Our results thus do not support the hypothesis that the high frequency of endophyte infections in natural populations is explained by improved germination. For example, Clay (1987) found that seeds of infected agronomic perennial ryegrass and tall fescue germinated 10% more than uninfected seeds. Instead, our results corroborate those of Bacon (1993), where infection did not increase germination of tall fescue. Increased percent germination, however, is only one of several purported benefits of harboring asexual, systemic endophytes (e.g., Clay 1987, 1990). Arizona fescue does not show some of these other benefits such as increased herbivore resistance (Saikkonen et al. 1998, Faeth and Sullivan 2003). However, infection may increase fitness of host related to other aspects of water availability. For example, infection may increase post-germination survival of seedlings at low soil water (Faeth and Bultman 2002, Faeth et al. 2002). Tests of how water availability affects seedling survival and adults await future experiments.

Like big sacaton, germination of Arizona fescue was delayed as osmotic potential became more negative (Fig. 5). However, delays began in Arizona fescue at less negative osmotic potentials than big sacaton and appear similar to the delays that McGinnies (1960) found in several species of *Agropyron*, another native, cool-season grass genus. These results suggest that although total germination of Arizona fescue remains relatively high through declining osmotic potentials, the timing of germination is sensitive to low osmotic potentials. Delays may be due to inhibitors present in the seeds. After physiological dormancy is broken, low osmotic potentials may result in delayed germination because of the longer time needed to leach out chemical inhibitors (Baskin and Baskin 1998b). Another possibility is that the seeds may need to absorb a specific amount of water to begin and continue the physiological processes involved in germination.

Big sacaton and Arizona fescue appear to germinate under a wide range of water stress. Future research should focus on seedling survival and establishment of these native grasses at varying osmotic potentials. Both grass species have been used in restoration projects on native grasslands in the southwestern United States and in revegetation attempts on disturbed areas (Pearson 1923, Nicholas and McGinnies 1982, Richter and Stutz 2001). Basic understanding of the requirements for germination and plant establishment of native species is vital for the success of these restoration projects. This is especially important in semi-arid regions where favorable conditions for germination and establishment may be rare (Briede and Mckell 1992, Brown 1995). In Arizona, for instance, conditions favorable enough for successful seeding may occur as infrequently as 1 in 10 years (Brown 1995). Understanding the parameters for germination of native seeds is a first step in determining the optimum time and conditions for restoration attempts.

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56: 623-626 November 2003

Brassica elongata ssp. *integrifolia* seed germination

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Abstract

Repeatedly during the late 19th and early 20th century, exotic weeds were introduced to the sagebrush (*Artemisia*)/bunchgrass rangelands of the Great Basin. Once established these weeds became invasive, spreading without the conscious efforts of humans. *Brassica elongata* ssp. *integrifolia* (Boiss.) Breistr. offers evidence this process of introduction still continues. *Brassica elongata* ssp. *integrifolia* is native to southeastern Europe and Asia. It was first collected in North America near Portland, Ore. in 1911. This initial infestation apparently did not persist. The next collection was near Eureka, Nev. in 1968. Currently, *Brassica elongata* ssp. *integrifolia* has spread about 200 km east and west along U S Highway 50 and 100 km north and south of the highway along secondary roads. As a first step in understanding the seed and seedbed ecology of this new invasive weed we investigated the germination of seeds at a wide range of constant and alternating temperatures. This plant produces abundant seeds that germinate over a wide range of constant and alternating temperatures. Maximum germination ranged from 84 to 94% depending on the year of seed production. Germination was extremely limited at very cold seedbed temperatures and low at the cold category of seedbed temperatures. Germination at these temperature is a competitive advantage for other exotic species on Great Basin rangelands.

Resumen

A fines del siglo 19 e inicios del siglo 20, en forma repetida, se introdujeron malezas exóticas a los pastizales de "Sagebrush" (*Artemisia*)/zacates amacollados de la Gran Cuenca. Una vez establecidas estas malezas vienen a ser invasoras, diseminandose si esfuerzos concientes del hombre. La especie *Brassica elongata* ssp. *integrifolia* (Boiss.) Breistr. ofrece evidencia de que este proceso de introducción aun continua. Brassica elongata ssp. integrifolia es nativa del sudeste de Europa y Asia, en Norteamérica fue colectada por primera vez en 1911 cerca de Portland, Ore., esta infestación inicial aparentemente no persistió; La siguiente colección fue cerca de Eureka, Nev. en 1968. Actualmente *Brassica elongata* ssp. *integrifolia* se ha diseminado 200 km al este y oeste a lo largo de la autopista US 50 y 100 km al norte y sur de la autopista a lo largo de caminos secundarios. Como un primer paso para entender la ecología de la semilla y de la cama de siembra de esta nueva especie de maleza invasora investigamos la germinación de la semilla en un amplio rango de temperaturas constantes y alternantes. Esta planta produce abundante semilla que germina en un amplio rango de temperaturas constantes y alternantes. La máxima germinación varió de 84 a 94%, dependiendo del año en que se produjo la semilla. La germinación fue extremadamente limitada en camas de siembra con temperaturas muy frías y baja en temperaturas catalogadas como frías. La germinación a estas temperaturas es una ventaja competitiva para otras especies exóticas en los pastizales de la Gran Cuenca.

Key Words: exotic weed, seedbed ecology, germination temperatures

Exotic weeds on rangelands are a cause of considerable concern because of the economic losses and ecological damage these species can produce. Recently, the exotic annual cheatgrass (*Bromus tectorum* L.) has provided fuel for huge wildfires in the Great Basin (Young et al. 1987). During the 1940s and 1950s, there was widespread alarm over the spread of the toxic exotic species halogeton (*Halogeton glomeratus* [M. Bieb.] C. Meyer) because of its destructive influence on the range sheep industry (Young et al. 1999). *Brassica elongata* ssp. *integrifolia* (Boiss.) Breitr. is proof that these endless cycles of introduction and spread are not complete (Young et al. 2003).

According to *Flora Europea*, *Brassica elongata* is native to southeastern Europe and Asia (Tutin et al. 1964). In Asia, it is found in southern Russia, the Ukraine, and the Republics of Central Asia as well as Turkey and Iran. In Asia, *B. elongata* occurs in semi-arid environments very similar to the sagebrush (*Artemisia*) zone environments of the Great Basin. There are 2 subspecies of this weed in its native distribution. The European form has divided to the mid-rib leaves and is known as *B. elongata ssp. elongata* Ehrh. Most species of *Brassica* that have established as exotic weeds in North America have basal leaves that are pinnatifid and leaves on the stem that are dentate (Munz and Keck 1959). The subspecies *elongata* was first described from specimens collected in Hungary (Rollins 1980). The plant that was introduced to Nevada is *B. elongata* ssp. *integrifolia* (Boiss.) Breistr., the subspecies from the semi-arid regions of Asia. The basal leaves of this subspecies are entire.

Brassica elongata was first collected in the United States in 1911 by Wilhelm Suksdorf at Linnton near Portland, Ore., in an area where ballast was unloaded from ships (Rollins 1980). We are not sure in which subspecies the Oregon collection belonged. This population apparently did not survive and the plant was considered to not occur in North America. In 1968 the noted American botanist John Thomas Howell was driving across central Nevada on U S Highway 50. He noted a plant in flower along the highway west of Pancake Summit in Eureka County (Rollins 1980). This specimen was deposited in the Gray Herbarium, misidentified as *Thelypodium* (Rollins 1980).

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Manuscript accepted 4 Feb. 02.

Based on herbarium specimens listed by Rollins (1980), and those housed at the University of Nevada Herbarium, and our own surveys, the current distribution of *Brassica elongata* is from Antelope Valley in Eureka County, east along U S Highway 50 for 200 km. It extends north and south of the highway along secondary roads for 100 km. The infestations are to the best of our knowledge restricted to roadsides. The plants are well established in portions of the road right-of-ways where native secondary successional species such as rabbitbrush (*Chrysothamnus* sp.) and squirreltail (*Elymus elymoides* [Raf.] Swezey) exist, indicating soil disturbance has not occurred for several years. The remarkable part of this distribution is the rugged topography and variety of plant communities it encompasses. The valley floor where the original collection was made is 1846 m in elevation with salt affected soils and 150 to 200 mm of highly variable annual precipitation. To the east along Highway 50 an infestation occurs at 2320 m elevation where the highway passes through pinyon (*Pinus monophylla* Torr. & Frem.)/juniper (*Juniperus osteosperma* [Torr.] Little) woodlands with mountain big sagebrush (*Artemisia tridentata* subspecies *vaseyana* [Rydb.] Beetle) in openings in the woodland.

Our purpose is to investigate the seed germination of *Brassica elongata ssp. integrifolia* at a wide range of constant and alternation incubation temperatures. This will give some understanding of the possible range of adaptation of this species.

Methods

We collected seeds in 1999 from a population of *Brassica elongata* growing along Highway 50 in the upper portion of Copper Flat in White Pine County, Nev. (Latitude N. 39° 00' Longitude W. 115° 30'). The elongated stand covers about 2 ha. Seeds were collected from about 100 plants. In 2000, seeds were collected from a much larger population in Newark Valley, Eureka County on the road to the Fish Creek Ranch (Latitude 39° 00' Longitude 114° 30'). This is probably an extension of the stand where John Thomas Howell made his original collection.

In all experiments 4 replications of 25 seeds each were used in a randomized block design. Seeds were placed on top of non-toxic commercial germination paper in closed Petri dishes and kept wet with tap water. Germination trials were conducted in the dark. Seeds were considered germinated when the radical emerged 1 mm. Germination counts were made after 1, 2, and 4 weeks. Constant incubation temperatures were 0, 2, and 5° C and at 5 degree increments through 40° C. Alternating regimes included 16 hours at each constant temperature, plus 8 hours at each possible higher temperature per 24 hours. For example, 35° C alternated with 40° C only, while 0° C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40° C. This made a total of 55 constant and alternating temperature regimes (Young et al. 1991).

The germination responses of the accessions of *Brassica elongata* were compared using the following seedbed temperature regime definitions (Young and Evans 1982):

a. Very cold: 0/0 (constant 0° C), 0/2 (0° C for 16 hours and 2° C for 8 hours in each 24hours), 0/5 and 2/2° C.
b. Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10° C.
c. Cold fluctuating: 0/20 through 0/40° C and 2/20 through 2/40° C.
d. Fluctuating: 5/35 through 5/40° C, 10/35, 10/40, and 15/40 C.
e. Moderate: 5/20 through 5/30, 10/10 through 10/30° C, 15/15 through 15/35° C, 20/20 through 30/35° C, and 25/25 through 25/30° C.
f. Warm: 20/40, 25/35, and 25/40° C, 30/30 through 30/40° C, 35/35, 35/40, and 40/40° C.

The temperature categories reflect germination environments of field seedbeds based on several years of monitoring in the Great Basin (Evans et al. 1970, Evans and Young 1970, 1972).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 1% level of probability (Young et al. 1980, Evans et al. 1982, Palmquist et al. 1987). A number of germination parameters were calculated from the quadratic response surfaces (Table 1) (Young and Evans 1982).

Results and Discussion

There were marked differences as well as similarities in the germination profiles for the seeds of *Brassica elongata* collected in different years (Tables 2, 3, and 4). The seeds were not collected from the same stand because the population used in

Table 1. Germination parameters calculated from quadratic response surfaces (Young and Evans 1982).

Calculated parameters	Derivation of parameter	Purpose
Calculated within profile:		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination	Number with germination divided by 55	Indication of breath of germination response
Percentage of regimes with optima	Number of regimes with germination not less than the maximum observed minus one half the confidence interval divided by 55	Provides indication of the breath of temperatures that support optimum germination
Mean of optima	Sum of optima divided by number of regimes with optima	Provides a measure of potential germination at most desirable temperatures
Maximum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles		
Frequency of optima	Times a given temperature supports optimum germination divided by the total number of test	Provides an estimate of optimum temperatures for germination with precision

Table 2. Mean germination of seeds of *Brassica elongata* ± one half of the confidence interval at the 0.01 level of probability. Incubation for 4 weeks at a wide range of constant and alternating temperatures. Seeds produced in 1999.[1]

Cold period temperature	Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
(C)	(%)									
0	0+10	0+10	0+10	0+10	2±8	10±8	24±6	26±8	16±8	0+10
2		0+10	0+10	0+10	7±8	26±8	33±8	56±8	34±10	0+10
5			0+10	2±8	2±8	9±10	28±10	61±4	42±6	0+10
10				9±10	18±8	14±6	44±4	43±3	29±8	0+10
15					15±8	25±8	43±6	68±8	66±6	34±6
20						48±8	64±6	56±6	65±6	40±10
25							64±6	67±8	[84±9]*	40±10
30								18±10	22±8	16±8
35									5±8	5±11
40										0+10

[1] Number following the mean is one half of the confidence interval as determined from regression equations used to develop the response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. * indicates means not lower than the maximum germination minus one half of its confidence interval, our definition of optimum germination.

Table 3. Mean germination of seeds of *Brassica elongata* ± one half the confidence interval at the 0.01 level of probability. Incubation for 4 weeks at a wide range of constant and alternating temperatures. Seed produced in 2000 .[1]

Cold period temperature	Warm period temperature C									
	0	2	5	10	15	20	25	30	35	40
(C)	(%)									
0	0+12	0+12	1±10	27±8	45±6	62±6	66±6	32±6	32±6	0+10
2		0+12	1±10	3±10	20±8	40±8	77±6	70±6	58±6	2±10
5			2±10	6±10	31±8	60±8	71±6	78±4	66±6	2±10
10				5±8	27±8	54±8	65±6	66±6	68±6	10±8
15					68±6	[94±6*	94±6]*	86±6	86±6	23±8
20						62±6	67±6	58±8	58±8	38±8
25							74±6	66±6	59±8	59±8
3								9±6	15±8	21±10
35									2±10	20±10
40										0+12

[1] Number following the mean is one half of the confidence interval as determined from regression equations used to develop the response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets [ ]. * indicates means not lower than the maximum germination minus one half of its confidence interval, our definition of optimum germination.

1999 did not produce sufficient seeds in 2000. The collection sites were located within 30 km of each other, but had a difference of 430 m in elevation, with the 2000 collection being the lower site. For both collections, none of the seeds germinated at very cold incubation temperatures. In the Great Basin, precipitation generally occurs in the winter when temperatures are too cold for plant growth. Generally, the seeds of successful exotic species have the potential to germinate at very cold seedbed temperatures and this has been interpreted as evidence of a competitive advantage over seeds of many native species (i.e. Young and Evans 1977). There also were marked differences between the collections of *Brassia elongata* in germination at cold, cold fluctuating, and moderate temperatures (Table 4). Only at moderate and warmer temperatures was the average germination similar for the 2 collections.

From an over all view point, the seeds of *Brassica elongata* have some germination at a remarkably broad spectrum of temperatures (76 to 94% of the 55 temperature regimes tested, Table 2). The maximum germination of 84 to 94% that was observed indicates the seeds have a high potential to germinate with little dormancy at optimum temperatures for germination. The populations we sampled differed in temperatures that supported optimum germination (Table 4). The high elevation population had 84% germination at 25/35° C (25° C for 16 hours and 35° C for 8 hours in each 24 hours). The lower elevation population had 94% germination at 15/20 and 15/25° C.

Table 4. Germination parameters (standard error at the 0.01 level of probability) calculated from germination profiles for seeds of *Brassica elongata* collected in 1999 and 2000.

Germination parameter	Year seed produced	
	1999	2000
	(%)	
Profile mean	20 ± 2.3	30 ± 3.1
Regimes with some germination	76 ± 4.1	93 ± 4.9
Mean of optima	84 ± 5.1	94 ± 2.1
Regimes with optima	2 ± 2.1	4 ± 2.3
Maximum germination	84 ± 5.1	94 ± 3.7
Seedbed temperature categories		
Very cold	0	0
Cold	1 ± 4.1	13 ± 4.7
Cold fluctuating	23 ± 5.1	45 ± 4.9
Fluctuating	21 ± 3.4	34 ± 4.0
Warmer	27 ± 2.6	28 ± 3.8
Moderate	45 ± 6.1	61 ± 3.9

There is nothing in the temperature-germination profiles that is severely limiting except for the lack of germination at very cold temperatures. We have no idea where the species was first introduced in east central Nevada. The original collection site is on the far western side of the current known distribution. The distribution to the east and south is into a region where summer precipitation from monsoonal storms is consistent enough that it is probably much more biologically effective than further west in the Great Basin. The current known distribution of *Brassica elongata* may reflect the distribution of summer precipitation.

The area where this exotic species is now found contains irrigated farms where quality grass hay is produced for horses and it has been widely marketed in the western United States. As range and weed control scientist and technicians become more aware that *Brassica elongata* is established in the Great Basin, its range in western North America will be better known.

It is probably too late to eradicate this new exotic species, but existing populations could be greatly suppressed by weed control and revegetation programs. Many land management and agricultural people downplay the potential significance of this relatively new exotic species because it is largely confined to roadside environments. If you look back at the serious exotic, invasive weed species on the western range, it is easy to document references that virtually all exotic species were at one time confined to roadside environments. The roadside environment provides a temporary habitat while the exotic species evolves adaptation to its new environment.

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56: 627-633 November 2003

Herbicide effects on vegetation spatial patterns in a mesquite savanna

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Abstract

Several studies have examined the impact of woody plant (i.e., brush) management efforts on mesquite (*Prosopis glandulosa* Torr.) cover and associated ecological impacts, but little research has been done on spatial attributes of vegetation following mesquite management treatments. This study examined the effects of above-ground mortality (triclopyr or 2,4,5-T) and whole-plant mortality (clopyralid or triclopyr+clopyralid) mesquite herbicide treatments on the canopy cover and spatial pattern of vegetation in a mesquite savanna and the associated ecological and management implications. A GIS and landscape analysis based on classified color-infrared aerial photos were used to quantify the spatial patterns of woody and non-woody vegetation. The results indicate long-term (> 20 year) persistence of disturbance effects on the amount and spatial pattern of woody vegetation. Significant differences in spatial pattern were found between the herbicide treatments and the non-treated plots, as well as between the above-ground mortality (AGM) and whole-plant mortality (WPM) herbicide treatments. The differential changes in the amount and spatial distribution of woody cover under different treatments resulted in substantially different spatial distributions of non-woody vegetation with respect to distance to nearest woody vegetation. These spatial variations may influence production and zonation of herbaceous vegetation due to modified shading and root competition from mesquite. Our results support observations of differential rates of mesquite seedling recruitment and establishment between treatment types. We conclude that consideration of spatial pattern should be an important component of future brush management plans.

Key Words: brush management, clopyralid, spatial pattern analysis, GIS and remote sensing, semi-arid rangeland

Resumen

Varios estudios han examinado el impacto de los esfuerzos de manejo de las plantas leñosas (i.e. arbustos) en la cobertura de "Mesquite" (*Prosopis glandulosa* Torr.) y los impactos ecológicos asociados, pero poca investigación ha sido hecha sobre los atributos espaciales de la vegetación después de los tratamientos de manejo del "Mesquite". Este estudio examinó los efectos de la mortalidad aérea (triclopir or 2,4,5-T) y la mortalidad total de la planta (clopiralid o triclopir+clopiralid) en tratamientos de herbicidas para control de "Mesquite" en la cobertura de copa y patrón espacial de la vegetación en una savana de "Mesquite" y las implicaciones ecológicas y de manejo asociadas. Se uso un análisis de SIG y de paisaje basado en fotografías aéreas clasificadas de color-infrarrojo para cuantificar los patrones espaciales de la vegetación leñosa y no leñosa. Los resultados indican una persistencia a largo plazo (> 20 años) de los efectos de disturbio en la cantidad y patrón espacial de la vegetación leñosa. Se encontraron diferencias significativas en el patrón espacial entre los tratamientos de herbicidas y las parcelas no tratadas, así como entre los tratamientos de herbicida para mortalidad aérea (AGM) y mortalidad total de la planta (WPM). Los cambios diferenciales en la cantidad y distribución espacial de la cobertura leñosa bajo los diferentes tratamientos resultó en distribuciones espaciales substancialmente diferentes de la vegetación no leñosa con respecto a la distancia de la vegetación leñosa mas cercana. Estas variaciones espaciales pueden influir en la producción y zonificación de la vegetación herbácea debido al sombreado modificado y la competencia de raíz del "Mesquite". Nuestros resultados soportan las observaciones de tasas diferenciales de establecimiento de plántulas entre los tipos de tratamientos. Concluimos que la consideración del patrón espacial debe ser un componente importante de futuros planes de manejo de arbustos.

Shrub expansion into savanna and grassland systems over the past century has been documented throughout the world, including Texas and the southwestern United States (Grover and Musick 1990, Schlesinger et al. 1990, Archer et al. 1988, 1995, 2000, Ansley et al. 2001a). An important brush species in Texas and much of the southwestern United States is honey mesquite (*Prosopis glandulosa* Torr.). The increasing amounts of woody plants like mesquite have many ecological and management implications, including competition with herbaceous plants and associated reduction in forage availability (Dahl et al. 1978, Scifres et al. 1982, Bedunah and Sosebee 1984, Dye et al. 1995, Scholes and Archer 1997), changes in hydrology (Blackburn 1983, Wu et al. 2001), impacts on habitat of creatures ranging from soil microarthropods (Whitford and Sobhy 1999) to elf owls (Hardy et al. 1999) and feral hogs (Ilse and Hellgren 1995), plant species composition shifts (McPherson et al. 1988) and soil nutrient cycling (Knoop and Walker 1985, Connin et al. 1997, Gill and Burke 1999).

While many studies have examined the impact of mesquite control treatments on the abundance (i.e., cover and density) of

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This project was partially supported by the National Science Foundation through a Graduate Research Fellowship Award to Heaton, and by the Texas Agricultural Experiment Station. The W.T. Waggoner Estate, Vernon, Tex. provided the land area for the research. Authors wish to thank R.A. Masters, R. Feagin, and 2 anonymous reviewers for their constructive review comments that helped to improve the manuscript.

Manuscript accepted 24 Jan. 03.

mesquite (Brock et al. 1978, Scifres et al. 1982, Herbel et al. 1983, Bedunah and Sosebee 1984, Heitschmidt et al. 1986), little work has been done on the impact of these treatments on the subsequent spatial pattern of mesquite. An exception is Ansley et al.'s (2001a) study documenting the rate of change of mesquite cover as well as spatial variables (patch density, mean patch size, distance to nearest neighbor, mean shape index) over 20 years on a non-treated site as compared with a root-plowed site. Spatial variables may offer a more explicit description of an ecological system than consideration of percent cover (abundance) alone; the same amount of mesquite can be arranged in dramatically different ways, with impacts on ecological processes as well as management concerns. Spatial pattern may point to potential long-term landscape-level shifts in vegetation dynamics.

The use of various herbicides and herbicide combinations, and their effectiveness for control of honey mesquite and other woody species, have been extensively documented as summarized by Bovey (1998, 2001). Triclopyr (3,5,6-trichloro-2-pyridinyloxyacetic acid, butyoxyethyl ester) and 2,4,5-T [(2,4,5-trichlorophenoxy) acetic acid] have been shown to successfully cause above-ground mortality (AGM), often resulting in basal resprouting of mesquite (Fisher et al. 1959, Dahl et al. 1978, Jacoby and Meadors 1983), while clopyralid (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt) has shown a greater ability to kill both the above-ground portions and roots of mesquite, resulting in whole-plant mortality (WPM) (Bovey and Whisenant 1991, 1992).

The objective of this study was to examine the long-term effects of AGM and WPM herbicide treatments on the spatial patterns of woody and non-woody vegetation in a mesquite savanna. Changes in spatial patterns of vegetation may have important ecological and management implications.

Materials and Methods

Study Area

The research site was located on the W.T. Waggoner Ranch, about 37 km southwest of Vernon, Tex. (33°53' N., 99°21' W.; elevation 380 m), in the northern Rolling Plains ecoregion of Texas. The climate of the area is continental and semiarid. Mean annual precipitation is 65.2 cm at Vernon, with peak rainfall bimodally distributed in May and October. Mean annual air temperature is 17° C. Soils are fine, mixed, thermic Typic Paleustolls of the Tillman and Wichita series, which are alluvial clay loams from 0 to 3-4 m depth, underlain by Permian sandstone/shale parent material (Koos et al. 1962). Vegetation on the site is dominated by a woody overstory of honey mesquite. Other woody species include lotebush (*Ziziphus obtusifolia* var. *obtusifolia* [Hook. Ex T.&G.] Gray), tasajillo (*Opuntia leptocaulis* DC.), and plains pricklypear (*Opuntia polycantha* Haw.). The herbaceous species on the site are a mixture of cool-season (C3) and warm-season (C4) grasses. Primary cool-season grass species are the perennial midgrasses Texas wintergrass (*Nassella leucotricha* [Trin. and Rupr.] Barkworth.) and Texas bluegrass (*Poa arachnifera* Torr.), and the annual grass Japanese brome (*Bromus japonicus* Thunb ex. Murray). Warm season grasses are perennial short-grass buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.), and midgrasses silver bluestem (*Bothriochloa laguroides* [DC.] Herter. Subsp. *torreyana* [Steud.]), meadow dropseed (*Sporobolus compositus (Poir.) Merr.*), and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.). A moderate, continuous grazing regime has been in place for at least 50 years at a stocking rate of about 12 ha/cow (30 acre/cow).

Herbicide Treatment and Experimental Plots

The AGM (triclopyr or 2,4,5-T) or WPM (clopyralid or triclopyr + clopyralid) herbicides were aerially applied by a fixed-wing airplane to treatment areas within a set of pastures in 1977, 1979, 1987, and 1988 (Table 1) as a field test to evaluate the potential of various herbicides for mesquite control The treatments were applied in rectangular strips approximately 84 m x 400 m (about 3.4 ha) . Buffer strips (ca. 15 m) were left between treatments. The non-treated areas had no record of any brush control for more than 30 years; ranch records indicate that the entire pasture was aerially sprayed with 2,4,5-T in 1968. There was no internal fencing in the pasture, so cattle and wildlife were free to move across treatments. Canopy foliage, when averaged over all trees, was reduced equally by the AGM and WPM herbicide treatments (Table 1). The percentage of mesquite with AGM (all original stems killed and exhibiting basal re-growth) was slightly greater in the AGM than the WPM treatments in each spray year. Percent WPM (percent of mesquite with all original stems killed and exhibiting no re-growth) was substantially greater in the WPM than the AGM treatment, and greater in the WPM treatments applied in the 1970's than the 1980's.

The historical treatment setup and other alternations since then necessitated an unbalanced design for this study with unequal replications in each herbicide treatment and non-treated areas. Sixteen, 1-ha plots (each 71 x 141 m) were randomly located in each of 16 of the original 3.4 ha herbicide treatment strips. Of these 16 plots, 7 were in AGM treatments (4 in 12-year post-treatment and 3 in 22-year post-treatment areas), and 9 were in WPM treatments (5 in12-year post-treatment and 4 in 22-year post-treatment areas). Three other 1-ha plots were randomly located in untreated strips.

Development of Vegetative Cover Maps

Vegetative cover maps with woody and non-woody cover classes were developed from color infrared aerial photos taken on 2 September 2000 at a nominal scale of 1:5,000. The aerial photos were scanned into images with 0.5 m resolution and the images were geo-referenced using GPS coordinates taken in the field at points that were easily identifiable on the aerial photos.

To develop vegetative cover maps, the images were classified using the unsupervised classification procedure in ArcView

Table 1. Above-ground and whole-plant mortalities of herbicide treatments evaluated 2 years after herbicide application.

Herbicide Treatment	Year Sprayed	Canopy Reduction	Above Ground Mortality[1]	Whole Plant Mortality
	-------------------	-------------------	(%) -------------------	-------------------
AGM[2]	1977 or 1979	90 (2)[4]	33 (2)	4 (1)
AGM	1987 or 1988	87 (4)	45 (19)	2 (1)
WPM[3]	1977 or 1979	91 (3)	18 (6)	68 (4)
WPM	1987 or 1988	87 (5)	31 (6)	37 (2)

[1] Plants with complete original stem mortality then basally re-sprouted.

[2] AGM = above-ground mortality herbicide treatment using 0.56 kg ha^{-1} triclopyr or 2,4,5-T.

[3] WPM = whole-plant mortality herbicide treatment using 0.56 kg ha^{-1} clopyralid or 0.28 kg ha^{-1} clopyralid +0.28 kg ha^{-1} triclopyr.

[4] Standard error is shown in parentheses.

Image Analysis. This classification method uses the Iterative Self-Organizing Data Analysis (ISODATA) technique to identify and group similar pixels based on the reflectance values of the pixels (ERDAS 1998). Forty (40) classes (groups of similar pixels) were generated with a convergence threshold of 95% (ERDAS 1998). These 40 classes were then manually assigned to either woody or non-woody categories using the original color infrared images as reference. Given that the overwhelming majority of the woody canopy cover consisted of mesquite (Ansley et al. 2001b), it was assumed that all woody vegetation on the images was mesquite.

Classification accuracy was assessed using visual interpretation of the aerial photos at 415 randomly selected points within the plots. The overall accuracy (Jensen 1996) of the classification (correct assignment of pixels into woody or non-woody classes) of aerial photographs was 89.2%. The producer's accuracy (measure of omission error) was 85% for woody and 92% for non-woody, while user's accuracy (measure of commission error) was 89% for woody and 90% for non-woody. One likely source of error is that some of the smallest mesquite plants with sparse canopy were not detected in the classification process, although every effort was made to include as many as possible while maintaining the accuracy of the rest of the classification.

Analysis of Patch-Based Spatial Pattern

The spatial patterns of both woody and non-woody vegetation were quantified using 6 landscape variables: percent cover, mean patch size (m^2), patch density (number of patches ha^{-1}), mean shape index, mean nearest neighbor distance (m), and edge density (meters ha^{-1}). Shape index is a measure of patch shape complexity defined as $0.25*P/A^{1/2}$, where P is the perimeter and A is the area of the patch (McGarigal and Marks 1995). The shape index equals 1 for a square patch, the simplest raster shape, and increases when the shape of a patch becomes more complex. Nearest neighbor distance is the shortest edge-to-edge distance measured between a given patch and the nearest neighboring patch of the same type. Edge density is the total linear distance of all edges divided by the landscape area, expressed as meters of edge per hectare. It is important to note that a patch was defined as an area of continuous canopy, not an individual plant. One patch may encompass several mesquite trees if any parts of the canopies of these trees overlap in an aerial projection. Analyses of the spatial pattern of the vegetative cover map for each of the 19 plots were conducted using the ArcView Patch Analyst extension (Elkie et al. 1999) that was developed based on the landscape analysis software FRAGSTATS (McGarigal and Marks 1995).

Statistical tests of the effect of the herbicide treatments on the spatial pattern were conducted using the General Linear Model (GLM) procedure and specific contrasts in SAS (SAS 1994). A 1-way analysis of variance with 5 treatment levels (AGM-12 yr, AGM-22 yr, WPM-12 yr, WPM- 22 yr, and non-treated) was conducted using GLM for each of the 6 landscape variables for woody and non-woody patches, respectively. Five specific contrasts, AGM-12 yr vs. AGM-22 yr, WPM-12 yr vs. WPM-22 yr, AGM vs. non-treated, WPM vs. non-treated, and AGM vs. WPM, were conducted for each landscape variable of each vegetative cover type with significant overall treatment effects. A significance level of $\alpha = 0.05$ was used for all statistical tests and was adjusted for the contrasts based on Bonferroni inequality (SAS 1994).

Frequency distribution of patch size and frequency distribution of distance to the nearest woody pixel from each non-woody pixel for each treatment type were also developed. This information was used to account for potential masking of interesting patterns due to the averaging of patches over the hectare plots.

Lacunarity Analysis

To obtain an integrative measure of change in underlying landscape pattern between treatment types, a lacunarity curve was developed for each of the 19 plots. Lacunarity is a metric of landscape texture and measures the deviation of a geometric structure from translational invariance, or the "gappiness" of a geometric structure (Plotnick et al. 1993). Lacunarity analysis has been used to quantify landscape patterns and their dynamics in rangeland studies (Wu et al. 2000, Derner and Wu 2001). Lacunarity was calculated using a procedure (Wu and Sui 2001) implemented in ArcView Spatial Analyst extension based on the "gliding box" algorithm (Allain and Cloitre 1991, Plotnick et al. 1993). To calculate lacunarity, the hectare vegetative cover maps were reclassified, assigning woody pixels a value of 1 and non-woody pixels a value of 0. Lacunarity is calculated at multiple scales for a given landscape, in this case using gliding boxes with side length of 0.5, 1, 2, 4, 8, 16, and 32 m. A box of given side length r was placed in 1 corner of the hectare map, and the sum of the values of all pixels contained within the box, called the "box mass" S(r), was calculated. The box was moved across the entire grid at 1-pixel intervals and the box mass determined at each location. Lacunarity (L) for box size r was calculated as 1 plus the ratio of the variance and the mean square of the box mass for size r: $L(r) = var[S(r)] / E[S(r)]^2 + 1$. A lacunarity curve, consisting of a log-log plot of lacunarity L(r) against box size r, was generated for each plot to quantify the spatial pattern of the landscape at a range of scales. The range over which rapid decrease of lacunarity occurs, as indicated by the lacunarity curve, may indicate a domain of scale for a given landscape beyond which the spatial pattern becomes random. (Plotnick et al. 1993, Dale 2000).

The proportion of the landscape occupied by the habitat of interest (in this case, percent woody cover) influences lacunarity values, at least at small scales, because a higher percent cover will lead to higher mean box mass and therefore lower lacunarity values than a lower percent cover. To examine the pattern and scaling of spatial heterogeneity determined by spatial configuration independent of percent cover, lacunarity curves can be normalized to factor out the effect of percent cover (Plotnick et al. 1996). Normalized lacunarity curves were generated by rescaling the corresponding lacunarity curves, dividing the lacunarity value L(r) at each box size r by the value for box size 1 (ln[L(1)]), so each curve would start at r = 1 and L(r) = 1, and eventually approach 0 (Plotnick et al. 1996). Analysis of variance and specific contrasts using GLM procedure (SAS 1994), similar to those used above for patch-based landscape variables, were used to test the effect of herbicide treatments on lacunarity value and normalized ln(lacunarity), respectively, at each spatial scale (Derner and Wu 2001).

Results and Discussion

Herbicide Effects

Significant differences in landscape variables were found between the herbicide treatments and the non-treated areas, as well as between the above ground mortality (AGM) and whole plant mortality (WPM) herbicide treatments (Table 2), while there was no significant difference between 12- and 22-year post treatments of AGM or WPM for any of the landscape variables. Both AGM and WPM herbicide treatments significantly altered the long-term abundance and spatial pattern of woody and non-woody vegetation as compared with non-treated areas. Significant differences were also found between the 2 treatment types in percent cover, patch density and mean shape index (woody only).

For woody vegetation, WPM plots exhibited a high density of well-dispersed (large mean nearest neighbor distance) small patches with relatively simple shapes in comparison to AGM plots, which had a less dense arrangement of larger patches with more complex shapes, and non-treated plots with low densities of large, contiguous patches with relatively complex shapes (Table 2). The more complex patch shapes in the AGM than the WPM treatment are a reflection of basal regrowth from established root systems in the AGM treatment. The greater percent cover in the AGM than the WPM treatment is likely also due to a higher occurrence of basal re-growth in the AGM than in the WPM treatment. However, because not all mesquite were completely killed in the WPM treatment (Table 1), some mesquite in this treatment also had basal regrowth following treatment.

Mean woody patch size was greatest in the non-treated areas due to the presence of relatively old, large trees and coalescing/overlapping canopies of adjacent trees. The presence of large and complex woody patches formed by old multi-stemmed trees, often with overlapping canopies, is also indicated by the significantly higher mean shape index in the non-treated areas than in either herbicide treatment. In contrast, the relatively large non-woody mean patch size and mean shape index in the WPM treatment areas as compared to AGM and non-treated plots (Table 2) indicate a highly continuous and complex herbaceous matrix in the WPM treatment areas. The herbaceous component in the AGM areas is less continuous, while the herbaceous component in the non-treated areas is highly fragmented and consists of small, dispersed, non-woody patches in a highly continuous woody matrix. Ninety-eight percent (98%) of the woody area in non-treated plots occurred in patches larger than 1,000 m^2, while only 12% of the woody area in WPM plots occurs in this size class (Fig. 1a). In contrast, there were no non-woody patches larger than 1000 m^2 in the non-treated plots while patches of this large size made up 98% of the non-woody pixels in WPM plots and 74% of the non-woody pixels in AGM plots (Fig. 1b).

Edge density was considered as a potentially important variable due to findings by Brock et al. (1978) of differing herbaceous species composition in 3 zones surrounding mesquite plants. A higher amount of edge may lead to more abundant transition zone vegetation. Despite the large differences in the percent cover and other spatial variables, edge density of mesquite was not significantly different between treatment types. This is likely due to the large number of small woody patches in the treated areas with lower percent woody cover, relative to the few large woody patches in non-treated areas with high percent woody cover (Table 2).

Simultaneous consideration of multiple landscape variables of percent cover, mean patch size, patch density, mean shape index, as well as the frequency distributions of patch size and distance to woody pixels, captures different aspects of spatial pattern and paints a more ecologically meaningful picture than consideration of any one of these variables singularly. Since lacunarity reflects both the attributes of the patches and their spatial arrangement in landscapes, lacunarity curves can integrate the information captured in these multiple landscape variables and provide a concise and multiple-scale representation of the differing landscape patterns of the various treatments. The WPM plots had the highest lacunarity values, followed by AGM plots, and non-treated plots had the lowest lacunarity values (Fig. 2a). The significantly higher lacunarity values in WPM than AGM and non-treated areas at all but the largest scales indicate a wide range of non-woody gap sizes and a high level of spatial heterogeneity or aggregation of the landscape

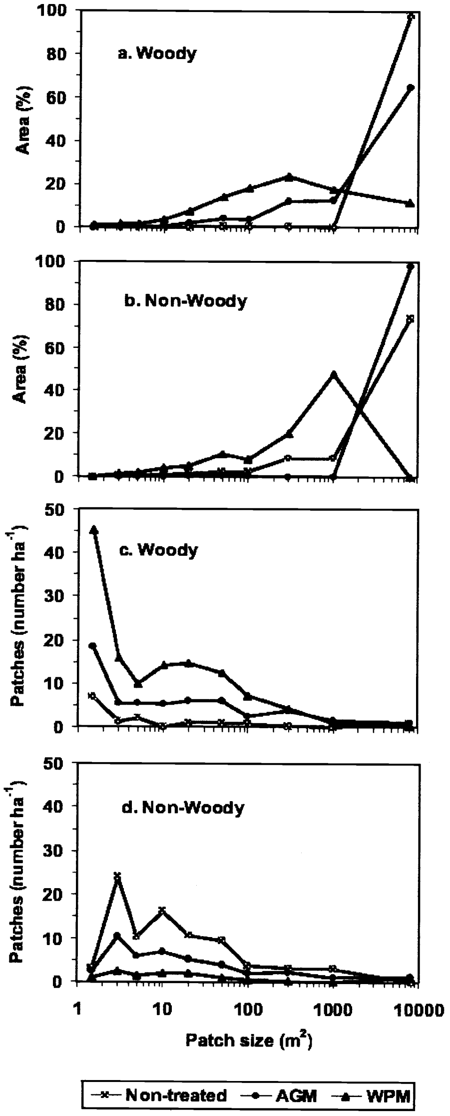

Fig. 1. Patch size distribution for woody (a,c) and non-woody (b,d) patches in the above-ground mortality (AGM) and whole-plant mortality (WPM) herbicide treatment (12- and 22-year post treatment combined) areas as compared with the non-treated areas. Size classes used were: 0–1.4. 1.5–2.9, 3.0–4.9, 5.0–9.9, 10–19.9, 20–49.9, 50–99.9, 100–299.9, 300–999.9, 1,000–2,999.9, and 3,000–10,000 m^2. Panels (a) and (b) illustrate the percentage of woody or non-woody area accounted for by each patch size class; panels (c) and (d) illustrate number of patches within each size class per hectare.

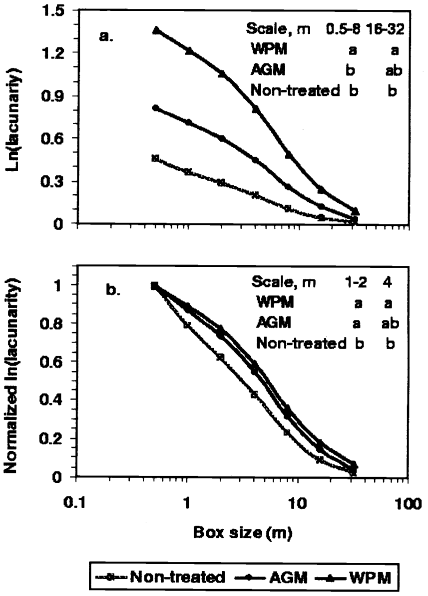

Fig. 2. Lacunarity curves (a) and normalized lacunarity curves (b) for above-ground mortality (AGM) and whole-plant mortality (WPM) herbicide treatments (12- and 22-year post treatment combined) and the non-treated areas. Significant ($\alpha = 0.05$) differences between curves are denoted by different letters at specific dates.

Table 2. Mean values of landscape variables for woody and non-woody components of the aboveground mortality (AGM) and whole-plant mortality (WPM) herbicide treatment[1] areas and the non-treated areas.

	Woody			Non-woody		
	Non-treated	AGM	WPM	Non-treated	AGM	WPM
Cover (%)	71^{a}[2]	49^{b}	28^{c}	28^{a}	50^{b}	71^{c}
Patch density (number ha–1)	14^{a}	56^{a}	125^{b}	84^{a}	41^{b}	12^{c}
Mean patch size (m2)	549^{a}	128^{b}	25^{b}	34	221	1074
Mean shape index	1.70^{a}	1.50^{a}	1.36	1.33	1.58	2.20
Mean nearest neighbor dist. (m)	1.38	1.66	1.84	2.03	1.29	1.32
Edge density (m ha–1)	2689	2958	2804	2467	2943	2935

[1] Data in AGM and WPM columns include both 12- and 22-year post treatment plots. There was no significant difference between 12- and 22-year post treatment groups of AGM or WPM for any of the landscape variables.

[2] For landscape variables with significant treatment effect, significant differences ($\alpha < 0.05$) between treatment types within woody or non-woody component are indicated by different superscript letters.

in WPM relative to the other 2 treatment types. This reflects the pattern of fragmented woody cover with many small patches (single- or few-stemmed recruits) and some larger patches where plants that survived the WPM treatment exhibit multi-stemmed regrowth. The non-treated areas had the lowest lacunarity values because of higher cover and more even spatial distribution of the woody vegetation. When lacunarity curves were normalized to factor out the effect of percent cover, the difference between normalized lacunarity curves for WPM and AGM became insignificant; however, both curves were significantly greater than that for non-treated plots at intermediate scales and had larger domains of scale than that of the non-treated plots (Fig. 2b). Normalized lacunarity curves demonstrate persistence of the underlying difference in the pattern and scaling of the landscape configuration between the treated and non-treated areas, and similarity between the WPM and AGM areas, regardless of percent woody cover.

Seedling Recruitment and Establishment

Treatment of WPM or AGM may lead to differential seedling recruitment and establishment rates. Field observations indicated that many more small, single-stemmed trees were growing in WPM areas than in AGM areas dominated by multi-stemmed plants, presumably from resprouting subsequent to mortality of above-ground material. This general observation, which has not been quantified in published studies of which we are aware, is supported by the results of the spatial analyses in this study, namely the smaller mean woody patch size, more dispersed distribution, higher woody patch density and lower mean shape index in WPM as compared to AGM plots (Table 2).

The mean patch size was significantly smaller in WPM treatments (25 m^2) than in non-treated plots (549 m^2), and also showed a trend (although non-significant) toward smaller size than AGM treatments (128 m^2). Not only were the mean patch sizes different, there were also considerable differences in patch size distribution among non-treated, AGM, and WPM plots (Fig. 1). For the smallest size class (area 1.5 m^2 or smaller), WPM plots averaged 45 woody patches ha^{-1}, compared to 18 woody patches ha^{-1} in AGM plots and 7 woody patches ha^{-1} in non-treated plots (Fig. 1c). Very few non-woody patches of area 1.5 m^2 or smaller were found in any of the 3 plot types; however, in the next size class (1.5m $\leq$ area $\leq$ 3m) there are 10 times more non-woody patches per hectare in the non-treated than in the WPM plots (24 vs. 2.5) (Fig. 1d).

The smaller mean patch size and larger mean nearest neighbor distance of the WPM areas (Table 2) and frequency distribution of distance from each non-woody pixel to the nearest woody pixel (Fig. 3) indicate not only smaller but also more dispersed mesquite in these areas. The frequency of distance from each non-woody pixel to the nearest woody pixel was most evenly distributed among various distances in WPM plots, while AGM and non-treated plots had a majority of pixels within 0.5 m of a woody pixel; 81% of the pixels in the non-treated plots and 61% of the pixels in AGM plots were within 0.5 meter of a woody pixel, while only 39% of the pixels in WPM plots were located this close to the nearest woody pixel (Fig. 3). At every measured distance from nearest woody pixel greater than 0.5 m, WPM plots had a higher percentage of pixels than both AGM and non-treated plots.

Mean nearest neighbor distance in the woody component also indicated a more dispersed pattern of woody vegetation, the mean distance between neighboring woody patches increasing from non-treated to AGM to WPM plots, although no significant treatment effect was found (Table 2); in the non-woody component, there was a trend toward longer nearest neighbor distances in non-treated plots than in either AGM or WPM plots (Table 2).

Woody patch density was significantly higher in WPM plots (125 ha^{-1}) than in AGM (56 ha^{-1}) or non-treated plots (14 ha^{-1}) (Table 2). High density of smaller patches possibly reflects the presence of many isolated mesquite recruits from seed whose canopies do not overlap with those of adjacent mesquite. The low woody mean shape index values for the WPM plots indicated the simplest mesquite canopy shapes among the three treatment types. This would be expected for plots characterized by a high proportion of single- to few-stemmed plants emerged from seed rather than multi-stemmed growth forms

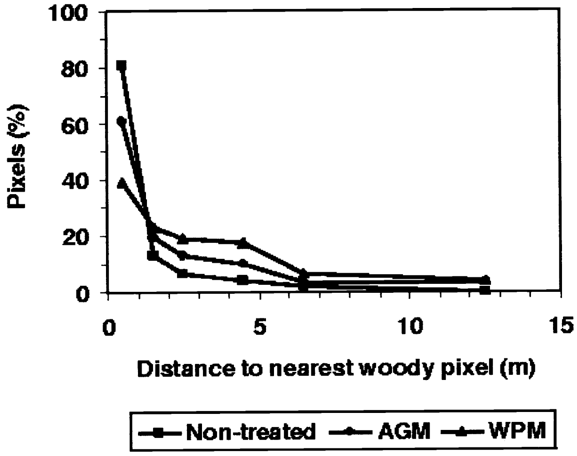

Fig. 3. Frequency distribution of distance from every non-woody pixel to the nearest woody pixel, for above-ground mortality (AGM) and whole-plant mortality (WPM) herbicide treatments (12- and 22-year post treatment combined) and the non-treated areas.

with more complex shapes resulting from resprouting after AGM herbicide treatment.

Changes in recruitment and establishment of mesquite following herbicide treatments might be due to reduction of competition from lateral roots following high rates of whole-plant mortality in WPM treatment areas. Studies have demonstrated the large areal extent of mesquite lateral roots (Heitschmidt et al. 1988, Scholes and Archer 1997) as well as the importance of these roots to the overall water use by mesquite (Ansley et al. 1990, 1998). The competition of mesquite for water resources is not limited to the area immediately surrounding each mesquite tree, but occurs in the interstitial areas between trees as well (Ansley et al. 1990, 1998, Scholes and Archer 1997). Reduction of this competition following WPM treatments may lead to increased opportunity for recruitment and establishment of new seedlings, as opposed to non-sprayed areas where little whole-plant mortality occurs, or AGM treatments where re-growth from stem bases rapidly restores competitive influence.

The process of recruitment of mesquite seeds is facilitated largely by livestock (cattle) dissemination of mesquite seeds via fecal deposition, although many wildlife species from deer to coyote may also contribute to this process (Brown and Archer 1987, Kramp et al. 1998). Seeds may be transported several hundreds of meters, if not kilometers, from the source plant through this process. Mesquite seeds must be scarified prior to germination, and passage through animal digestive systems provides this scarification. Seeds deposited in fecal matter are also advantaged by the ready nutrient-rich growth medium. It is likely that the experimental design may have encouraged dispersal of seed into the more open WPM areas. There are no fences between the various treatments, and animals (both domestic cattle and wildlife) roam freely throughout the site, with access to non-treated areas that provide shade and are an abundant source of mesquite seeds. Herbaceous production tends to be highest in open WPM areas (Dahl et al. 1978, Bedunah and Sosebee 1984, Ansley et al. 2001b), therefore animals (cattle and wildlife) may potentially spend more time grazing in these areas, and defecating mesquite seeds that they may have ingested.

Management Implications

The higher percent woody cover in the above ground mortality (AGM) versus the whole plant mortality (WPM) areas, likely due to the basal sprouting of mesquite plants following application of AGM herbicides, may have considerable impact on forage production (Dahl et al. 1978, Herbel et al. 1983, Laxson et al. 1997), and is therefore of interest for management considerations of livestock production and wildlife. In addition to differences in percent cover, the spatial pattern of mesquite following treatment, which can influence the level of competition between mesquite and herbaceous species, has direct implications for production in the herbaceous layer. Spatial patterns of mesquite, such as patch density, size, and arrangement may influence animal movement and foraging behavior (Etzenhouser et al. 1998) and the level of difficulty in herding livestock.

The significant differences found between non-treated areas and areas of up to 22 years post-treatment indicate considerable longevity of the herbicide treatments. This agrees with estimates of treatment longevity of at least 20 years used in studies of the economics of brush control in this region of Texas (Whitson and Scifres 1981). Differing spatial attributes were most pronounced between the non-treated and the WPM plots, indicating a greater impact of WPM than AGM herbicides on woody vegetation amount and spatial pattern. These results are supported by a recent study of the economics of mesquite control with herbicide application in the Rolling Plains region of Texas, in which WPM treatments were found to be economically viable and AGM treatments were not, despite the higher treatment cost of WPM (ca. $59/ha) vs. AGM (ca. $37/ha) application (Teague et al. 2001).

Differing patterns of woody vegetation resulting from treatment may lead to different properties of mesquite savannas in the future, depending on subsequent management decisions. A high density of small patches may lead to more abundant dense stands of mesquite in WPM areas as trees grow larger, or a more open understory may result from growth of single-stemmed seedlings as opposed to multi-stemmed regrowth from existing crowns. The implications for future characteristics of a mesquite savanna will change depending on follow-up treatments subsequent to initial herbicide spraying.

Conclusions

Significant differences were found in percent cover and spatial pattern of woody and non-woody vegetation in a honey mesquite savanna in northern Texas, between non-treated plots and the herbicide treatments for mesquite control, as well as between the 2 different treatments, one yielded high above ground mortality and low whole plant mortality (AGM treatment) and the other yielded high whole plant mortality (WPM treatment). Differing spatial pattern was illustrated by simultaneous consideration of multiple landscape metrics.

Lacunarity analysis was effective for quantifying and differentiating the spatial patterns of different treatments at multiple scales. Normalized lacunarity curves, which factored out the influence of varying amounts of woody cover between treatment types and the non-sprayed areas, demonstrated that the brush control treatments considered had an impact on the underlying spatial pattern of vegetation, regardless of percent cover. This changed spatial pattern may influence long-term ecology and management of brush control treatments.

Results from spatial analysis support observations of a higher level of seedling recruitment in the WPM plots than in either the AGM or non-treated plots. These differential recruitment rates may be a function of reduced competition from mesquite lateral roots in the WPM plots and possibly increased seed dispersal into the WPM plots via fecal deposition by cattle moving freely among the treated and non-treated areas.

Spatial patterns of vegetation have not been widely considered in the mesquite management literature, which has focused on the response of herbaceous vegetation to mesquite removal. Differing spatial patterns and patch attributes following mesquite herbicide treatments may have important impacts on current ecological processes as well as the future characteristics of mesquite savannas. Spatial patterns of mesquite resulting from different treatments should be an important consideration in the design and decision-making of long-term mesquite management practices.

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J. Range Manage.
56: 634-639 November 2003

Defoliation, waterlogging and dung influences allocation patterns of *Deschampsia caespitosa*

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Abstract

Wet meadows are some of the most productive communities in the northern Rocky Mountains, USA but are also among the most sensitive to grazing by native ungulates and domestic livestock. These meadows typically are inundated with floodwater in spring and early summer but are relatively dry in summer. To determine the interactive effects of clipping and flooding on plant recovery after clipping, we subjected plants of tufted hairgrass (*Deschampsia caespitosa* (L.) Beauv) to 6-week and 10-week waterlogging treatments in combination with 1 and 2 clipping events, with and without dung amendment in a greenhouse experiment. The experiment was designed to mimic early and late growing-season patterns of herbivory by native and domestic herbivores on a dominant species of wet meadows of this region. Waterlogged plants produced a higher percentage of roots at the surface, elongated stems to the first axial leaf, increased the proportion of tillers that flowered, but increased aboveground yield and tiller height only with the addition of dung. Root biomass declined with waterlogging when dung was not added, and a second defoliation exacerbated the negative effects of waterlogging on roots. Defoliation with short-duration waterlogging increased shoot nitrogen (N) concentration and N yield/root biomass, while continuous waterlogging reduced shoot N concentration of aboveground biomass. Dung amendment did not reverse this effect. Although extended flooding in combination with moderate rates of defoliation did not reduce aboveground biomass of *Deschampsia caespitosa*, it aggravated total root loss, caused shifts to a shallower root distribution, and altered N concentration of aboveground biomass for herbivores.

Resumen

Las praderas húmedas son una de las comunidades mas productivas del norte de las Montañas Rocallosas del E.U.A, pero también están entre las mas sensitivas al apacentamiento por ungulados nativos y ganado doméstico. Estas praderas típicamente están inundadas en primavera e inicios de verano pero son relativamente secas en el verano. Para determinar el efecto interactivo del corte y la inundación en la recuperación de las plantas después del corte condujimos un experimento de invernadero en el que sometimos plantas de "Tufted hairgrass" (*Deschampsia caespitosa* (L.) Beauv) a tratamientos de inundación de durante 6 y 10 semanas en combinación con 1 o 2 eventos de corte y con y sin la aplicación de estiércol El experimento se diseñó para simular los patrones de herviboría de inicios y fin de la estación de apacentamiento de los herbívoro nativos y domésticos sobre las especies dominantes de las praderas húmedas de esta región. Las plantas inundadas produjeron un mayor porcentaje de raíces en la superficie, alargaron los tallos en la primer hoja axilar, incrementaron la proporción de hijuelos que florecieron, pero incrementaron el rendimiento de la biomasa aérea y la altura de los hijuelos solo con la adición de estiércol. La biomasa de raíz disminuyó con la inundación cuando no se adiciono estiércol y una segunda defoliación exacerbó los efectos negativos de la inundación en la raíz. La defoliación con cortos periodos de inundación incrementó la concentración de nitrógeno de los tallos (N) y el rendimiento de N/biomasas de raíz, mientras que la inundación continua redujo la concentración de N en los tallos de la biomasa aérea. La incorporación de estiércol no invirtióeste efecto. Aunque la inundación en periodos largos en combinación con tasas moderadas de defoliación no redujeron la biomasa aérea de *Deschampsia caespitosa* si agravó la perdida total de raíz, causo cambios hacia una distribución de raíz mas superficial y alteró la concentración de N de la biomasa aérea para los herbívoros.

Key Words: flooding, tufted hairgrass, herbivory, nitrogen dynamics, wet meadows

Riparian and wet meadow systems are among the most productive foraging areas for both native ungulates and domestic livestock in the western rangelands of the United States; yet they are also among the most sensitive of North American habitats to grazing impact (Johnson et al. 1977). These areas typically are inundated with floodwater in spring and early summer, but are relatively dry in late summer depending on snowpack and the timing of snow melt. Studies in upland systems have shown that plant recovery after defoliation depends largely on environmental conditions (Maschinski and Whitham 1989, Georgiadias et al. 1989), yet only a few studies (Middleton 1990, Oesterheld and McNaughton 1991, Gough and Grace 1998, Pacheco 2001) have addressed the effects of flooding on grazing responses outside the flooding Pampa of Argentina (Chaneton et al. 1988, 1996, Rubio et al. 1995, Chaneton and Lavado 1996, Insausti et al. 1999). None of these studies have addressed plants of the northern Rocky Mountain wet meadows.

Oesterheld and McNaughton (1991) suggested that the interactive effects of flooding and defoliation may be more detrimental

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Research was funded by the Basic Research Grants Program at the University of Wyoming.

Manuscript accepted 8 Oct. 02.

than either effect individually because plants adapted to defoliation or flooding induce largely opposite responses. For example, grazing-tolerant species often respond to defoliation by increasing photosynthetic rates, allocating resources to photosynthetic tissue over roots, and assuming a prostrate growth form (Caldwell et al. 1981, McNaughton 1984, Coughenour et al. 1985). On the other hand, when flooding occurs, roots and microbes rapidly consume available oxygen resulting in anoxic, reduced soils (Kozlowski 1984). Because anoxia interferes with root respiration, flood-tolerant species elongate their stems above the water and develop arenchymatous tissue to allow the transport of oxygen down the shoots to the roots (Crawford 1978); however, since phytotoxins may accumulate under reducing conditions, root permeability may constrain nutrient uptake and water absorption resulting in stomatal closure, reduced photosynthesis, and decreased production (Jackson and Drew 1984, Jackson and Hall 1987). Thus, flooding may hinder the normal plant responses to defoliation such that the timing and frequency of defoliation relative to flooding may be an important determinant of plant response in wet meadow systems.

We designed a greenhouse experiment to compare responses of *Deschampsia caespitosa* (L.) Beauv to a combination of defoliation and flooding treatments that mimic the conditions this species is subjected to under some management practices in mountain meadows of the northern Rocky Mountains, USA. Typically, domestic cattle are deferred from grazing mountain meadows until mid-summer, but native ungulates use the meadows before the arrival of cattle, moving to higher elevations when cattle arrive in the area (Yeo 1981, Kratville 1989, Kelly 1995). We chose to study tufted hairgrass (*Deschampsia caespitosa*) because it is a dominant bunchgrass in wet meadows found between 2,000 and 3,500 m in elevation throughout the Rocky Mountains, and is grazed by both elk and cattle (Kufield 1973). We hypothesized that: (1) an increase in the duration of flooding would decrease shoot and root biomass and N concentration; (2) plants defoliated more than once (i.e., similar to combined spring defoliation by elk and summer defoliation by cattle) do not recover as completely as when they are defoliated only once in the growing season, and continuous flooding exacerbates poor plant recovery; (3) flooding produces morphological traits resulting in a higher proportion of biomass vulnerable to further defoliation; and (4) dung amendment ameliorates declines in biomass and N concentration in flooded plants.

Material and methods

Tufted hairgrass plants were collected on 6 May 1993 in high elevational flooded meadows (2,250 m) near the Laramie River, 10 km west of Laramie, Wyo. (41° 18' 41" N, 105° 35' 26" W), USA. Plants were collected prior to green-up and transported to the greenhouse where tiller number was reduced to 25, dead leaf material was removed, and roots cut at 10 cm from the crown-root interface. Plants were placed in pots (20 cm diameter x 20 cm height) filled with soils collected from the site, and kept in a greenhouse maintained at 20° C. Sunlight during the day peaked at 811 W m^{-2} during the experimental period. Plants were watered daily and allowed to grow for 3 weeks prior to the experiment. Three tillers per plant were arbitrarily selected and marked for morphological measurements with thin (diameter < 0.5 mm), plastic-coated wire.

Experimental treatments were initiated on 26 May 1993 when the plants were assigned randomly within a 3 x 2 x 2 factorial design with 8 plants per treatment combination (n = 96). Factors and levels were 3 waterlogging treatments (none, 6 weeks [discontinuous], and 10 weeks [continuous]), 2 clipping regimes (clipping only once, clipping twice) and 2 fertilization treatments (none, dung amendment when clipped). We used these treatments in an effort to mimic patterns of herbivory in mountain meadows where native herbivores graze the meadows early in the growing season and then move to higher elevations; the meadows are then used by cattle during the remainder of the growing season (Yeo 1981, Kelly 1995). Flooding consisted of waterlogging potted plants within plastic tubs and maintaining the water level at 0–2 cm above the soil surface. Pots were re-randomized among flooding tubs every week without allowing the pots to drain. Non-waterlogged plants were watered daily with no additional nutrients added (other than the dung treatments). The first clipping occurred on 26 May while the second clipping occurred on 2 July. All aboveground biomass was removed above 10 cm from the soil line at each clipping. Fertilization consisted of applying wet weight of fresh elk dung after first clipping and cattle dung after second clipping. Fresh feces were collected from penned elk fed alfalfa at the University of Wyoming's Red Buttes Environmental Biology Laboratory and from cattle grazing shortgrass prairie near Laramie, Wyo. Dung samples were combined and mixed (as much as dung form would allow) prior to application. Based on Kjeldahl analysis (Bradstreet 1965) of percent N for 5 arbitrarily collected subsamples of each type of dung, N applied in elk dung was 53.7 kg/ha and cattle dung at 46.8 kg/ha.

Prior to plant harvest on 4 August 1993, we counted the number of vegetative and reproductive tillers per plant and measured height of marked tillers, distance from the soil line to the first basal leaf, number of leaves per vegetative tiller, and length of the first axial leaf. Harvested plants were separated into aboveground biomass, surface roots (< 2.5 cm from soil surface), and bottom roots (> 2.5 cm). Plant materials were oven-dried for 48 hours at 50° C, and weighed and analyzed for Kjeldahl N. Soil samples from just below the soil surface and at about 8 cm below the soil surface were taken from half of the plants in each treatment combination (n = 48) and analyzed for ammonium and nitrate at the University of Wyoming Soils Testing Laboratory using an autoanalyzer.

Analysis of variance and Tukey's highly significant difference test (Zar 1996) were used to detect differences in treatment means and interactions. Plant yield was determined as standing crop at harvest plus clipped biomass. Total N yield was estimated from above ground plant yield and N concentration at harvest. Except for tiller height, biomass and morphological measurements were transformed using a log transformation prior to analysis. Percent N values were transformed using arcsine square-root transformation prior to analysis because values were below 30% (Zar 1996). Differences were considered significant at $\alpha \leq 0.10$.

Results

Waterlogging had no effect on standing, aboveground biomass at the end of the experiment unless dung was added, and plant yield increased (160 to 240%) only with waterlogging and dung amendment compared to no flooding and dung treatments (Table 1, Fig. 1). Tillers of waterlogged plants were taller than non-waterlogged plants when they were not clipped a second time, and the height difference was most pronounced when plants were waterlogged and dung was not added (Fig. 2a). Twice clipping consistently reduced

Table 1. **Significance levels for ANOVA differences among treatment means and interactions among waterlogging (W), clipping (C), and dung amendments (D) on *Deschampsia caespitosa* (L.) Beauv ns = P > 0.10.**

	W	C	D	F x C	C x D	F x D	FxCxD
Aboveground yield	0.001	0.001	0.001	0.015	ns	0.001	ns
Aboveground biomass	0.001	0.005	0.001	0.013	ns	0.013	0.014
Total root biomass	ns	0.001	0.000	0.000	ns	0.000	.012
Surface root biomass (%)	0.017	ns	ns	ns	ns	ns	ns
Number tillers/plant	0.008	ns	0.001	0.091	ns	0.001	0.090
Reproductive tillers (%)	0.045	ns	0.001	ns	ns	0.001	ns
Tiller height	0.002	0.001	0.020	0.017	0.014	ns	ns
Leaves/vegetative tiller	0.001	0.041	ns	0.060	ns	0.001	ns
Leaf length	0.001	.001	.001	ns	ns	ns	ns
Distance to first leaf	0.001	ns	ns	ns	ns	0.001	ns
Green shoot N (%)	0.001	ns	ns	0.005	ns	0.001	ns
Surface root N (%)	0.030	ns	0.001	ns	ns	ns	ns
Basal root N (%)	0.000	ns	ns	0.008	ns	ns	0.025
N uptake (N in harvested + clipped biomass/root biomass)	0.001	0.001	0.016	0.001	ns	0.001	ns
Soil < 2.5 cm NH_4^+-N	0.031	ns	ns	ns	ns	0.012	ns
Soil < 2.5 cm NO_3^--N	ns	0.083	ns	ns	ns	ns	ns

leaf lengths while waterlogging increased leaf lengths. Dung amendment exaggerated these effects (Fig. 2b). Only waterlogging had an effect on the distance to the first axial leaf, with average distances increasing by 6–12 mm when no dung was added and 14–22 mm when dung was added (Fig. 2c). Waterlogging had little effect on the number of leaves/tiller when dung was added, but reduced the number of leaves on plants without dung that were clipped twice in the growing season (Fig. 2d). Waterlogging decreased the number of tillers and increased the proportion of reproductive tillers in plants (Fig. 3); however, the addition of dung reversed this effect.

Root responses varied even more by treatment than did aboveground growth. When dung was not added, total root biomass declined an average of 22% with discontinuous waterlogging and 33% with continuous waterlogging, with the greatest reduction observed in plants clipped twice in the growing season (Fig. 1). At the end of the experiment, root biomass was highest in plants that were discontinuously waterlogged, clipped only once in the season, and amended with dung. Plants exhibited a greater proportion of root biomass at the surface when plants were waterlogged (Fig. 1).

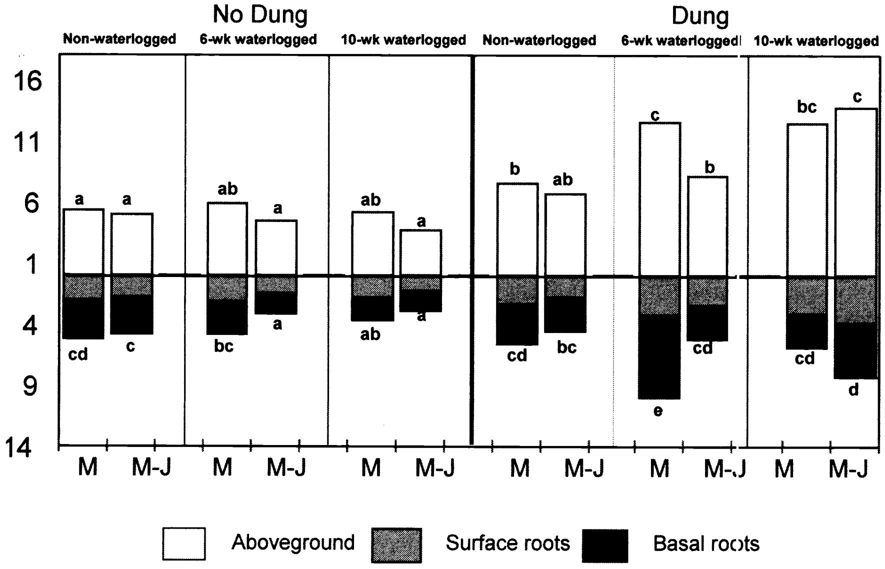

Fig. 1. Aboveground standing biomass and root biomass (g/plant) of *Deschampsia caespitosa* (L.) Beauv plants harvested 10 weeks after initiation of 3 treatments: waterlogging for 0, 6 and 10 weeks; clipping once in May (E) and once in May and July (L) clipping to 10 cm; and no dung addition or dung addition with clipping once or clipping twice. Surface roots were collected < 2.5 cm from soil surface. Means with the same letters are not significantly different at α = 0.10 across all treatments.

Continuous, but not discontinuous, waterlogging reduced shoot N at the end of the experiment, and dung amendment only partially ameliorated this effect (Table 2). Discontinuously waterlogged plants that were clipped twice had higher shoot N than plants clipped only once in the growing season. While this was consistent across dung treatments, the difference was significant only when dung was not added. Surface root N generally was higher when dung was added (Table 2). Nitrogen dynamics in basal roots were more complex. Overall, waterlogging reduced basal root N; the clipping regime influenced basal root N but only when dung was added. The nature of the effect depended on the duration of waterlogging. Nitrogen uptake, as reflected by the ratio of total N yield to root biomass, was higher in twice clipped plants and was most pronounced in plants that were discontinuously waterlogged (Table 2).

Ammonium ion concentration was higher (Paired t-test, $t_{df=94} = -2.026$, $P = 0.046$) in samples taken from the soil surface (0-2.5 cm) than in samples taken deeper in the soil, while there was no difference ($t_{df=94} = -1.365$ $P = 0.176$) in nitrate concentrations. Treatment differences in soil N occurred only in the upper, but not the lower soils (Table 2). Ammonium accumulated with flooding, whereas nitrate levels were lower in soils of plants clipped twice in the season.

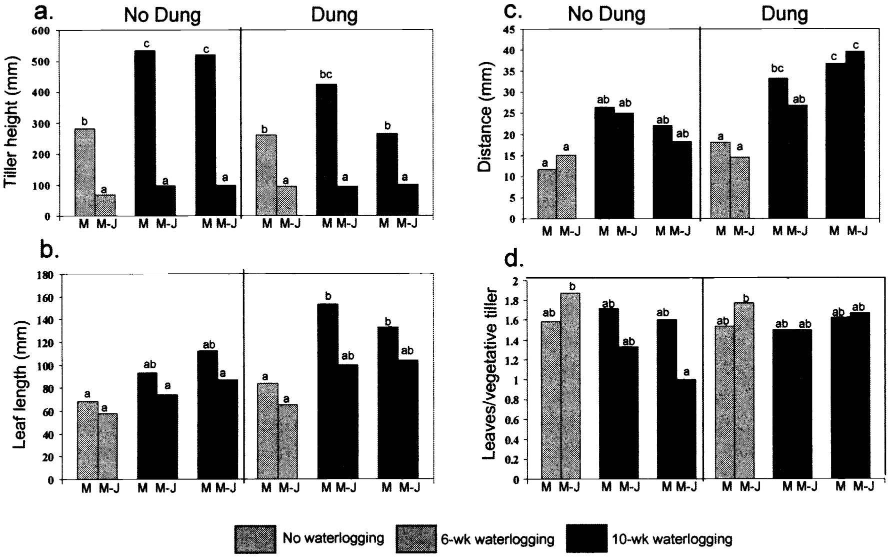

Fig. 2. Average tiller height (a), length of first axial leaf (b), distance from soil line to first axial leaf (c), and number of leaves/vegetative tiller (d) of *Deschampsia caespitosa* (L.) Beauv plants harvested 10 weeks after initiation of waterlogging, clipping and fertilization treatments. Treatments as described in Fig. 1. Means with the same letters are not significantly different at α = 0.10 across all treatments.

Discussion

Contrary to our hypothesis, duration of waterlogging neither reduced aboveground production nor aggravated the effects of a second defoliation on standing biomass or yield of tufted hairgrass under greenhouse conditions. Tufted hairgrass is characteristic of wet soils and is well adapted to anoxic soils associated with waterlogging (Lawrence 1945, Davy and Taylor 1974, Rahman 1976, Rahman and Rutter 1980, Theodose and Bowman 1997), but when subjected to heavy defoliation by ungulates, it generally is replaced by Kentucky bluegrass *(Poa sandbergii* L.) (Padgett et al. 1989). Clipping to a 10-cm stubble height was used in this study because this is the criterion sometimes used in mountainous areas of the northern Rocky Mountains of the USA for removing cattle from the range (Kelly 1995). At this level of defoliation, tufted hairgrass has the potential to recover from the combined effects of these disturbances, which may explain why it remains common in wet meadows where grazing is managed, but declines where grazing pressure is high (Padgett et al. 1989).

Oesterheld and McNaughton (1991) hypothesized that the negative interactive effects of flooding and grazing found in total yield of Serengeti grasses resulted from preferential allocation to support tissue (stems) because of their lower photosynthetic rates. Increased distance to the first axial leaf and tiller height observed in our experiment are generally consistent with this hypothesis, yet we found no reduction in aboveground biomass with flooding and defoliation. Instead, the increase in tiller height was associated with a shift to fewer, but taller, flowering tillers. Similar shifts in flowering culms have been reported for *Sporabolus virginicus* (L. Kunth.) in response to flooding (Naidoo and Naidoo 1992, Naidoo and

Table 2. Nitrogen yield/root (g/g), shoot, surface root, and basal root nitrogen (% N), and soil ammonium (NH_4^+) and nitrate (NO_3^-) concentrations (mg/kg) of soils collected < 2.5 cm and > 8 cm below the soil surface from pots in which Deschampsia caespitosa was grown. Treatments included 3 flooding levels (no flooding, 6-weeks, 10-weeks), 2 clipping frequencies (26 May, 26 May and 2 July), and 2 dung amendment levels (none, or elk dung with first clipping and cow dung with second clipping).

	N yield/root	Shoot N	Surface Root N	Basal Root N	Surface soil NH_4^+	Surface soil NO_3^-	Lower soil NH_4^+	Lower soil NO_3^-
	(g/g)	(%)	(%)	(%)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)
No dung amendment								
No flooding								
Clipped once	2.56ab	1.32b	0.83a	1.30ab	1.93ab	0.83ab	1.73	0.93
Clipped twice	3.06ab	1.28b	0.80a	1.34ab	1.03a	0.78ab	1.83	0.65
Intermittent flooding								
Clipped once	3.34ab	1.47b	0.95ab	1.26ab	2.15ab	0.90ab	1.40	0.87
Clipped twice	6.28c	1.82c	0.94ab	1.28ab	2.40ab	0.78ab	1.82	0.75
Continuous flooding								
Clipped once	2.46a	0.95a	0.85a	1.23ab	3.85ab	0.88ab	2.50	0.75
Clipped twice	3.44ab	0.87a	0.87a	1.19ab	5.88b	0.93ab	2.38	0.75
Dung amendment								
No flooding								
Clipped once	4.75bc	1.58bc	0.95ab	1.48b	2.35ab	1.08ab	2.50	0.83
Clipped twice	4.68bc	1.49bc	0.92ab	1.46b	2.78ab	0.90ab	2.05	0.78
Intermittent flooding								
Clipped once	2.37a	1.06ab	0.95ab	0.97a	5.45b	0.88ab	4.50	0.87
Clipped twice	5.57c	1.52bc	1.12c	1.38ab	3.15ab	0.75ab	2.55	0.87
Continuous flooding								
Clipped once	3.91b	1.21ab	1.08c	1.25ab	2.52ab	1.40b	1.95	0.87
Clipped twice	3.87b	1.05ab	1.01bc	1.02a	3.18ab	0.68a	1.77	0.85

[1] Different letters indicate significant (α = 0.10) differences among treatments within a column.

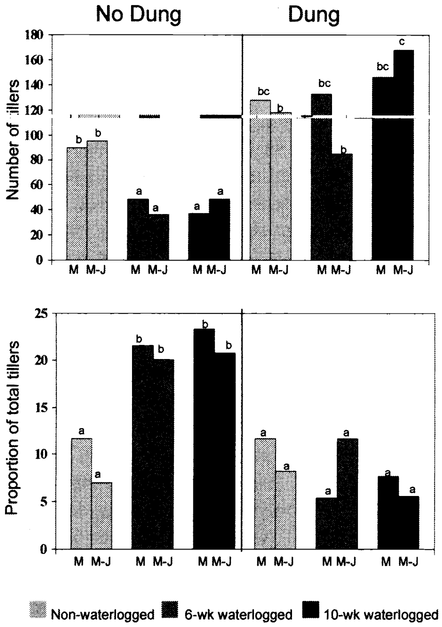

Fig. 3. Number of tillers per plant (a) and proportion of flowering tillers (b) of *Deschampsia caespitosa* (L.) Beauv plants harvested 10 weeks after initiation of waterlogging, clipping and fertilization treatments. Treatments as described in Fig 1. Means for above ground biomass and total root biomass with the same letters are not significantly different at α = 0.10 across all treatments.

Mundee 1993) and may be triggered by high ammonium concentrations in the surface soils (Ruess et al. 1983). Such a strategy can provide for seed bank enhancement or dispersal of seeds across flooded areas (Kirkman and Sharitz 1993).

In contrast to aboveground responses, waterlogging resulted in reductions in total root biomass as well as a change in root distribution when dung was not added. Although an increase in surface roots may promote oxygen diffusion to the rhizosphere, maintenance of total root biomass in anoxic, flooded soils typically requires a well-developed aerenchyma system. Tufted hairgrass is reported to have a moderately high capacity for aerenchyma in its roots, likely providing oxygen storage for short term needs, but is insufficient to maintain aerobic respiration under continual flooding (Crawford 1978).

Lower shoot N in continually flooded plants and increased plant production both above- and belowground with dung amendment indicates a nutrient limitation under continuous waterlogged conditions. Nevertheless, lower root:shoot ratios in flooded, tufted hairgrass plants indicate that lower root biomass under waterlogging sustained aboveground production (Fig. 1.). Likewise, laboratory experiments with barley plants have reported reductions in N uptake without reductions in dry matter accumulation when plants were flooded (Leyshon and Sheard 1975, Drew and Sisworo 1979). Oesterheld and McNaughton (1991) suggested that aboveground yield can be maintained in flooded plants by some degree of compensation in root function. Our estimates of aboveground N yield/root biomass support an increase in N uptake with defoliation, but not with flooding. Alternatively, the decline in N concentration without a decline in aboveground production in continually flooded plants may have resulted from increased N-use efficiencies that occur under relatively low nitrate soil levels (Jiang and Hull 1998) and that are associated with both an abundance of ammonium and an increase in flowering. Selection for flexible N-use efficiencies in flood-tolerant plants may be an important adaptation in productive wet meadow communities, since competition for light can be high and waterlogged soils limit nutrient uptake.

Despite the patchy distribution of dung, its importance in promoting plant production in wetland systems has been demonstrated in experimental applications of ammonium, nitrate, and goose feces in the field (Cargill and Jefferies 1984, Bazely and Jefferies 1985). Although the amount of dung we added to our pots was high, it was similar to what we observed in small areas around individual plants in wet meadows and fell within the range of 127–823 mg N/m^2 reported in areas intensively grazed by geese (Hik et al. 1991). The simplest explanation for increased growth in continuously flooded plants is that flooding makes soluble N, and other nutrients readily available to plants (Bazely and Jefferies 1985). The higher biomass of surface roots in flooded plants may facilitate N uptake at the oxidized soil-water interface when dung is deposited, making nutrient return by animals more readily available for plant in wet meadow systems compared to upland systems. Nonetheless, if flooding enhances nutrient availability where dung occurs, this does not appear to translate into higher N shoot concentration as has been found in upland systems with grazing (Holland and Detling 1990, Merrill et al. 1994). Instead, increased aboveground production with flooding had a diluting effect on shoot N concentration. Thus, while total N available to herbivores may increase, total N per bite may decrease.

High N yield/root biomass and shoot N under discontinuous flooding and clipping may involve several mechanisms. First, the rate of ammonium loss, which accumulated under flooding in the upper soil, may decrease under rapid drying of the soil (Ferguson and Kissel 1986). The pool of ammonium may have increased availability of nitrates under improved soil conditions. Nitrate diffuses more readily in the soil (Barber 1984) and is readily taken up by defoliated plants because clipping has a stimulatory effect on nitrate uptake (Ruess et al. 1983). We did not observe increased nitrate in discontinuously flooded soils; however, a decline in nitrate occurred with defoliation across treatments. Alternatively, root mortality associated with defoliation may create a readily available carbon source for microorganisms (Holland and Detling 1990, Merrill et al. 1994, Bardgett et al. 1998), which may result in high mineralization rates under improved aerobic conditions in the soil. Indeed, higher mineralization rates have been reported in the flooding Pampa that is grazed (Chaneton et al. 1996).

While our experiment does not replicate natural conditions, field observations on the aboveground response of tufted hairgrass to grazing and flooding independently support our results that hairgrass remains abundant under temporarily flooded conditions and under moderate grazing levels, but declines in unflooded uplands and under heavy grazing (Davy and Taylor 1974, Padgett et al. 1989). We know of no studies that have examined root responses to the combination of these factors in the field. Changes in biomass and nitrogen allocation patterns resulting from interactions among flooding, defoliation, and dung deposition may have several implications for wet meadow grazing systems. First, grazing to a particular plant height (e.g., 10 cm), as is commonly practiced (Kelly 1995, Dovel 1996), may produce higher rates of defoliation than believed because plant height increases with flooding; the amount of biomass removed in our clipping treatments was correlated with plant height (r = 0.73, P = 0.01, n = 96). Second, flooding can result in reduced root biomass, and a second defoliation appears to aggravate this loss. Finally, although flooding may not reduce aboveground plant production in tufted hairgrass communities under moderate defoliation (Bonham 1972), particularly where dung deposition is heavy, duration of flooding may play an important role in altering aboveground plant N concentration and N return to the animal.

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J. Range Manage.
56: 640-645 November 2003

Long-term effects of burning *Festuca* and *Stipa-Agropyron* grasslands

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Abstract

The effects of early spring burning on current year standing crop, litter, and total standing crop (current year standing crop plus litter) were examined in *Festuca*- and *Stipa-Agropyron*-dominated communities in central Saskatchewan over an 11-year period in a paired design with burned sites compared to adjacent control sites that were not burned. In *Festuca* communities current year standing crop was reduced in the first and third years ($P = 0.010$) after burning. Burning *Stipa-Agropyron*-communities tended to reduce current year standing crop, but the differences were not significant ($P < 0.050$) compared to control. Increasing precipitation stimulated current year standing crop after burning *Festuca* ($P < 0.001$, $r^2 = 0.33$) and *Stipa-Agropyron* ($P < 0.001$, $r^2 = 0.55$) communities. Litter and current year standing crop were correlated ($R^2 = 0.24$, $P = 0.002$) for *Festuca* indicating beneficial and detrimental effects of litter on production at low and high amounts, respectively. Litter and current year standing crop were not correlated ($P = 0.964$) for *Stipa-Agropyron*. In both communities total standing crop increased until about the eighth year after burning while the mass of litter appeared to reach a plateau around 11 years.

Key Words: *Agropyron dasystachyum*, Fescue Prairie, *Festuca hallii*, fire, litter, Northern Mixed Prairie, primary productivity, *Stipa curtiseta*, total standing crop

Resumen

Se examinaron los efectos de la quema a inicios de primavera sobre la cosecha en pie actual, mantillo y cosecha en pie total (cosecha en pie del año actual + mantillo) de comunidades de *Festuca* y comunidades dominadas por *Stipa-Agropyron* situadas en la región central de Saskatchewan. El estudio se llevo a cabo en un período de 11 años en un diseño apareado con sitios quemados adyacentes a sitios control que no fueron quemados. En las comunidades de *Festuca* la cosecha en pie actual se redujo en el primer y tercer años ($P = 0.010$) después de la quema. La quema de comunidades de *Stipa-Agropyron* tendió a reducir la cosecha en pie del año actual, pero las diferencias no fueron significativas ($P < 0.050$) en comparación con el control. El aumento en la precipitación estimuló la cosecha en pie del presente año después de la quema en las comunidades de *Festuca* ($P < 0.001$, $r^2 = 0.33$) y *Stipa-Agropyron* ($P < 0.001$, $r^2=0.55$). El mantillo y la cosecha en pie actual estuvieron correlacionadas ($R^2 = 0.24$, $P = 0.002$) en la comunidad de Festuca, indicando efectos benéficos y detrimentales del mantillo en la producción en cantidades bajas y altas respectivamente. El mantillo y la cosecha en pie actual no estuvieron correlacionadas ($P = 0.964$) en la comunidad de *Stipa-Agropyron*. En ambas comunidades la cosecha en pie total se incremento hasta aproximadamente el octavo año después de la quema mientras que la masa de mantillo pareció alcanzar su máximo nivel alrededor de los 11 años.

Prescribed burning is useful for achieving many conservation goals in grasslands. Beneficial effects of burning on production have been demonstrated in mesic grasslands such as Tallgrass Prairie where C4 grasses dominate (Wright and Bailey 1982, Collins and Wallace 1990). By contrast in the Northern Mixed Prairie and in Fescue Prairie dominated by C3 grasses, primary production is often reduced after burning (Redmann et al. 1993). For example, peak green biomass in Fescue Prairie recovered 2 to 3 years after burning, while in Mixed Prairie dominated by western porcupine grass (*Stipa curtiseta* Hitchc.) and northern wheatgrass (*Agropyron dasystachyum* [Hook.] Scribn.), recovery was delayed 4 to 5 years. Total graminoid biomass (green plus standing dead) in areas previously burned was comparable to unburned sites 3 to 4 years after burning, but recovery of litter took much longer in the Northern Mixed Prairie of western North Dakota (Dix 1960).

Litter alters the microenvironment of grasslands and affects productivity (Willms 1988, Facelli and Pickett 1991). Whereas excessive litter reduces productivity in Tallgrass Prairie (Vogl 1974, Boerner 1982), litter has positive effects on herbage production apparently by reducing evaporation and making more water available for plant growth especially in xeric Northern Mixed Prairie (Willms et al. 1986, 1993). Herbage production increased slightly with litter removal in Fescue Prairie but reductions in production occurred in Mixed Prairie (Willms et al. 1986). Climatic effects, particularly the amount of precipitation, also strongly influence primary productivity of Northern Mixed Prairie (Smoliak 1986) and Fescue Prairie (Bork et al. 2001).

Understanding the dynamics of standing crop of plants after burning is relevant to developing strategies for conserving *Festuca*- and *Stipa-Agropyron*-dominated grasslands. The purpose of this study was to examine the effects of burning over an 11-year period on current year standing crop, and the recovery over time of litter and total standing crop in Fescue Prairie and Northern Mixed Prairie dominated by western porcupine grass and northern wheatgrass.

Study site

This study was conducted at the University of Saskatchewan, Kernen Prairie located 1 km east of Saskatoon, Saskatchewan (52°10'N, 106°33'W; elevation 510 m). This 130-ha remnant

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Manuscript accepted 11 Mar. 03.

grassland has been relatively undisturbed since the 1930s except for periodic mowing on portions of it until 1976 (Pylypec 1986). Since 1986 various parts of the prairie have been burned by prescribed fires, and the impacts of these fires on the vegetation have been described in Redmann et al. (1993), Romo et al. (1993), Grilz and Romo (1994, 1995), Archibold et al. (1998) and Ripley and Archibold (1999).

Kernen Prairie lays in an ecotone between the Northern Mixed Prairie and the Boreal Forest. Therefore, the *Festuca*-dominated plant communities at Kernen Prairie are near the southern extent of their distribution while the *Stipa-Agropyron* communities are northerly extensions of typically more southern grasslands. Plains rough fescue (*Festuca hallii* [Vasey] Piper) dominates the more mesic sites with clayey glaciolacustrine soils within Kernen Prairie whereas western porcupine grass and northern wheatgrass dominate the more xeric sites at slightly elevated topographic positions with sandy loam soils (Baines 1973). A complete floristic inventory of Kernen Prairie is given in Pylypec (1986). Climate in this area has been described by Walter and Lieth (1960–1967) as Type VIII (VII), Boreal (Arid, with cold season). The mean annual temperature is 2.0° C, ranging from a January mean minimum of-22.9° C to an average maximum of 25.4° C in July (Environment Canada 1993). Normal annual precipitation is 347 mm of which 185 mm falls during the growing season (April–July).

Methods

A different portion of Kernen Prairie ranging from 4 to 16 ha was burned in the first 2 weeks of April each year from 1991 to 1997. At the time of burning prairie crocus (*Anemone patens* [Bess.] Koch) was in early stages of blooming. Burn areas included representative plant communities of Fescue Prairie (Coupland and Brayshaw 1953) and also of Northern Mixed Prairie (Coupland 1950), and were adjacent to similar controls where no fire has been recorded for the past eight decades.

Except for 2000, aboveground plant biomass at each burn site and the adjacent control area was sampled each year from 1991 to 2001 in late July to mid-August after green biomass had peaked. Previous studies in grasslands of this region have shown that peak standing crop is reached in late July to early August (Redmann et al. 1993, Zhang and Romo 1994, Kowalenko and Romo 1998). Four, 50- by 50-cm quadrats were randomly located along a 20 m transect in *Festuca*- and *Stipa-Agropyron*-dominated communities in each burn area and were compared to 4 quadrats of the same size in unburned control sites located within 20 m of the burns. In each quadrat, biomass was clipped at ground level and sorted into graminoids, forbs and shrubs. Fallen litter was collected from the surface by hand. All samples were oven-dried at 80° C for 24 hours and weighed. A subsample of the graminoids that comprised the bulk of the samples was then separated into green biomass, current year dead biomass and dead biomass from previous years; these subsamples were weighed and their proportions were applied to the entire sample. Graminoids comprised about 95% of the samples in *Festuca*-dominated communities and about 99% in *Stipa-Agropyron*-dominated communities. Current year standing crop was represented by the total of green biomass and current year dead biomass (Redmann 1992). Litter was determined as the sum of fallen, detached, and standing dead biomass from previous years. Total standing crop was the total of litter and current year standing crop.

Means of current year standing crop in control and burned plots were compared with 2-sample t-tests (Snedecor and Cochran 1980) within years after burning ($P \leq 0.050$). Regression analysis (Neter et al. 1990) was used to evaluate the relationships between: annual precipitation (August through July), growing season precipitation (April through July) and current year standing crop; litter and current year standing crop, and; the number of years since burning versus litter and total standing crop. Lack-of-fit tests ($P < 0.050$) (Snedecor and Cochran 1980) were used to select the best-fit regression equations.

Results and Discussion

Precipitation

Annual precipitation during the 11 years of study ranged from 18% less to 38% more than the normal of 347 mm. Precipitation was at least 10% greater than normal in 4 years, 90% or less than normal in 5 years, and within 10% of normal in 2 years. Thus, by repeating this study through time, responses of *Festuca*- and *Stipa-Agropyron*-dominated communities to burning were evaluated over wide-ranging amounts of precipitation in many combinations among years. Responses of current year standing crop, litter and total standing crop after burning discussed here are therefore applicable to a wide range of precipitation conditions.

Current year standing crop

Annual precipitation and current year standing crop were positively correlated ($P < 0.001$) after burning the *Festuca* and *Stipa-Agropyron* communities (Fig. 1). Correlations between current year standing crop and growing season precipitation were significant but lower than the correlation between annual precipitation and current year standing crop for *Festuca* ($Y = 82.5 + 0.40X$, $r^2 = 0.21$, $P < 0.001$) and *Stipa-Agropyron* ($Y = 20.2 + 0.53X$, $r^2 = 0.50$, $P < 0.001$). Increasing current year standing crop with precipitation was expected because precipitation constrains production in North American grasslands (Sims and Singh 1978). Herbage production also increases with precipitation in *Stipa-Bouteloua*-dominated grasslands (Smoliak 1986), grazed Fescue Prairie (Bork et al. 2001) and Tallgrass Prairie (Briggs and Knapp 1995). The variation in current year standing crop within precipitation amounts is attributed to harvesting being done in areas burnt in different years and they were therefore in different chronological stages of recovery after burning. Differences in production potential among burned areas likely also contributed to the variation in current year standing crop.

Burning mesic grasslands often stimulates production where conditions are often light- or nutrient-limited (Old 1969, Knapp 1984, Town and Owensby 1984, Abrams et al. 1986). However, current year standing crop in *Festuca* communities was reduced ($P < 0.050$) in the first and third years after burning (Table 1). A trend of less current year standing crop was observed after burning, but there was no difference ($P < 0.050$) compared to the control in the second year and after the third year. The longevity of reduced current year standing crop in the *Festuca* communities is close to a 2 to 3 year reduction reported by Redmann et al. (1993). On the other hand, current year production of plains rough fescue was not affected by burning in early April in Alberta (Gerling et al. 1995).

Despite a trend of less current year standing crop after burning, differences were not significant ($P < 0.050$) between control and burned *Stipa-Agropyron* communities within all years (Table 1). That burning had no effect on current year standing crop in *Stipa-Agropyron*-domi-

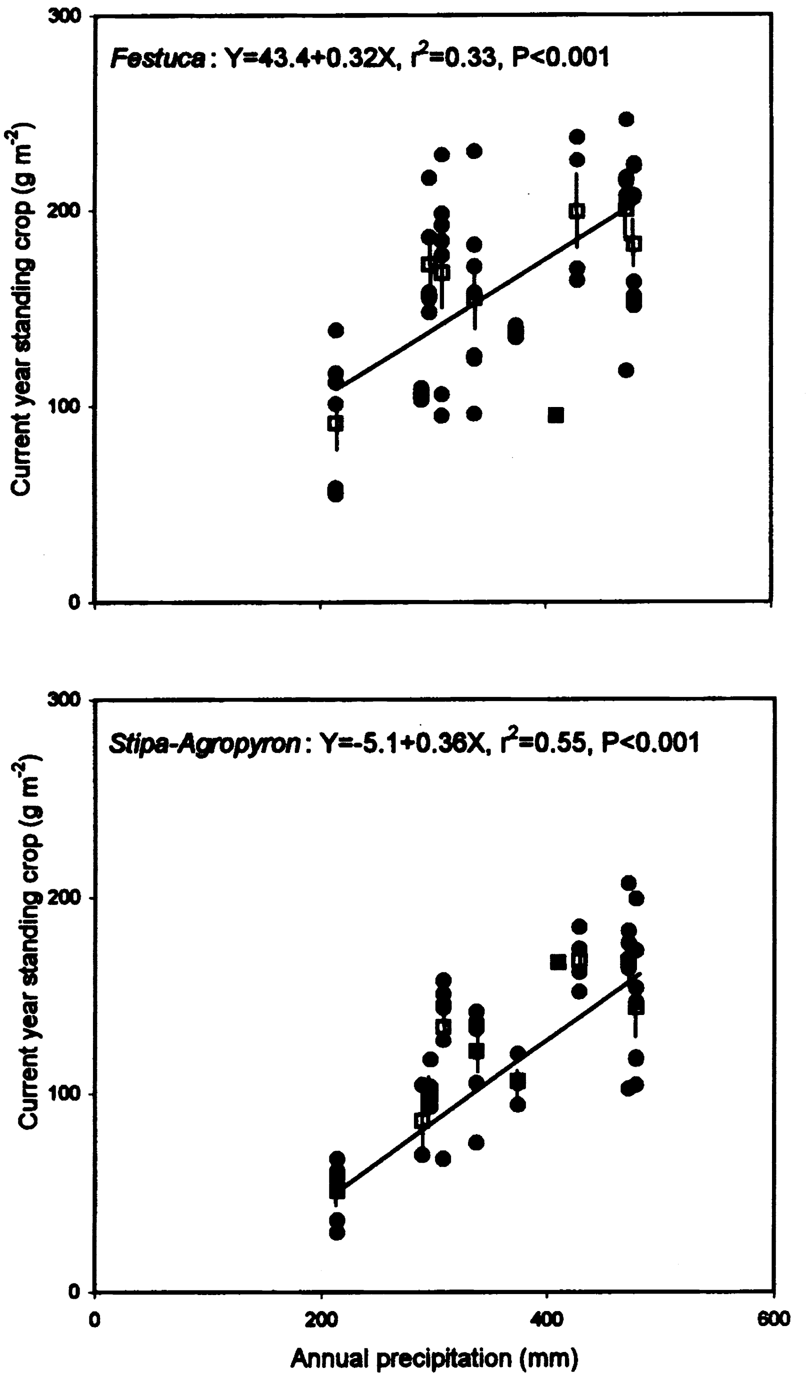

Fig. 1. Fitted regression lines and observed values for current year standing crop versus annual precipitation (August through July) in *Festuca*- and *Stipa-Agropyron*-dominated plant communities. Solid circles are observed current year standing crop and open squares with vertical lines are means ± SE for the control. Solid squares represent overlapping values for current year standing crop in control and after burning.

nated grasslands is at odds with earlier studies where productivity was reduced by burning (Redmann 1978, Engle and Bultsma 1984, Whisenant and Uresk 1989). Burning during a drought reduced current year standing crop of *Stipa-Agropyron*-dominated grasslands for 4 to 5 years (Redmann et al. 1993). Since the present study was conducted over a number of areas and years, and current year standing crop was measured over a wide range of environmental conditions, it is likely that variation in current year standing crop within years after burning masked the variation between control and burning. A similar response was also noted in Tallgrass Prairie (Briggs and Knapp 1995). Inherent differences among burned areas undoubtedly also contributed to variability in production within years after burning.

Current year standing crop after burning *Festuca* communities was correlated with the amount of litter ($Y = 83.5 + 0.71X - 0.0013X^2$, $R^2 = 0.24$, $P = 0.002$) (Fig. 2), but they were not correlated ($P = 0.964$) for *Stipa-Agropyron*. Deviation among observed current year standing crop is attributed to sampling being done during different years after burning and thus different growing conditions. The regression line in Fig. 2 suggests that low amounts of litter benefit production, large amounts are a detriment to production, and production is greatest at intermediate amounts. Willms et al. (1986) also noted increased total standing crop in Fescue Prairie after litter removal, and litter inhibits production in Tallgrass Prairie (Knapp and Seastedt 1986).

Altering the litter layer by burning may indirectly impact current year standing crop of *Festuca* communities by changing the microenvironment. Litter insulates the soil against incident solar radiation (Rauzi 1960, Willms et al. 1986, 1993) thereby reducing evaporation (Weaver and Rowland 1952, Hopkins 1954) and increasing soil water. Litter also insulates the soil, creating cooler temperatures in summer and warmer temperatures in winter (Johnston et al. 1971). Burning removes litter which in turn causes cascading effects of reduced soil water, increased plant water stress, and reduced production in Fescue Prairie (Redmann 1978, Redmann et al. 1993, Romo et al. 1993, Grilz and Romo 1994). We concur with Willms et al. (1986) that large amounts of litter appear to inhibit production and outweigh benefits of more soil water in *Festuca* communities. Even though our findings suggest that litter influences production in *Festuca* communities, additional studies are needed to elucidate relationships.

Production in drier parts of the Northern Mixed Prairie is associated with amounts of litter; production is maximized with maximum amounts of litter (Willms et al. 1986, 1993). Dix (1960) also concluded that litter does not inhibit production in Northern Mixed Prairie. In the present study, evidence suggests no improvement or reduction of current year standing crop in *Stipa-Agropyron* communities due to litter. The independence of current year standing crop and litter in *Stipa-Agropyron* indicates other factors, such as

Table 1. Current year standing crop in control and burned *Festuca*- and *Stipa-Agropyron*-dominated grasslands over the 11 years of study.

Growing seasons	*Festuca*					*Stipa-Agropyron*					
	Control		Burned			Control		Burned			
after burning	Mean	SE	Mean	SE	P	Mean	SE	Mean	SE	P	n
	---------(g m^{-2})--------		---------(g m^{-2})-------			---------(g m^{-2})--------		---------(g m^{-2})-----			
1	197a[1]	19.3	126b	10.5	0.01	144a[1]	6.5	114a	12.8	0.07	7
2	208a	23.8	152a	19.8	0.10	150a	14.5	116a	15.0	0.13	7
3	233a	13.7	167b	16.2	0.01	158a	15.8	131a	13.6	0.22	7
4	230a	12.3	192a	15.4	0.09	159a	13.0	142a	12.2	0.34	6
5	198a	24.6	190a	27.2	0.83	134a	16.1	121a	21.5	0.64	6
6	202a	31.7	163a	28.2	0.39	156a	28.1	142a	25.4	0.73	5
7	204a	13.5	171a	25.4	0.31	135a	20.6	131a	22.5	0.88	4
8	187a	29.8	131a	10.2	0.22	124a	37.7	131a	39.9	0.90	3
9	169a	46.5	146a	7.0	0.72	112a	66.0	86a	32.0	0.78	2
10	67	-----	112	-----	-----	103	-----	58	-----	-----	1
11	175	-----	55	-----	-----	70	-----	36	-----	-----	1

[1] Means followed by similar letters in the same row and plant community are not significantly different ($P<0.050$) between the control and burned plots.

precipitation, place greater controls on production than does litter.

Litter

Litter averaged 391 g m^{-2} (SE±12.4) in the *Festuca* control and 254 g m^{-2} (SE ± 8.6) in the control for *Stipa-Agropyron*. During the 11-year period litter increased in both *Festuca*- and *Stipa Agropyron*-dominated communities, with 79 and 78% of the variation in litter accounted for by years since burning (Fig. 3). Unexplained variation among observed values probably includes differences in production, transfer to litter, and decomposition among burn areas because observed amounts of litter are grouped by growing seasons after burning. In both *Festuca*- and *Stipa-Agropyron*-dominated communities, litter was reaching a plateau at the end of our study indicating about 11 years are required for the mass of litter to reach levels comparable to unburned sites. For the Northern Mixed Prairie in North Dakota it is estimated that mass of litter stabilizes in 11–16 years, depending on the plant community (Redmann 1975). At another location in North Dakota, litter recovered 4 years after burning *Stipa*-dominated communities while litter recovery took longer in *Agropyron*-dominated communities (Dix 1960).

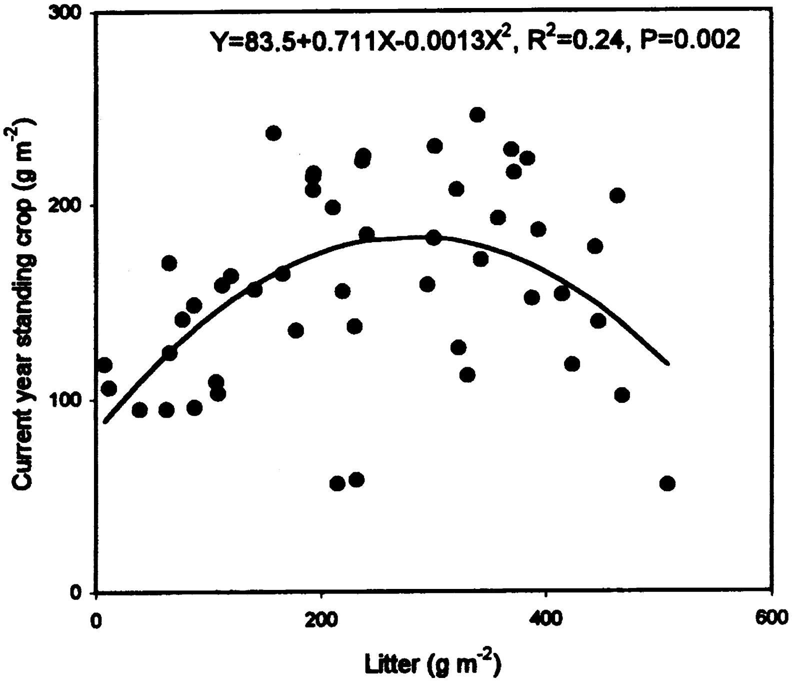

Fig. 2. The fitted regression line and observed values (solid circles) for current year standing crop and litter in burned *Festuca*-dominated plant communities.

Total standing crop

Over the 11-year period total standing crop in the control averaged 595 g m^{-2} (SE ± 14.5) in *Festuca*- and 398 g m^{-2} (SE ± 10.9) in *Stipa-Agropyron*-dominated communities. Total standing crop increased for about 7 to 8 years after burning before reaching a plateau in both communities (Fig. 4). The number of growing seasons since burning explained 67% and 58% of the variation in total standing crop in *Festuca* and *Stipa-Agropyron* communities, respectively. The unexplained variation in total standing crop is attributed to differences in production and decomposition among burn areas because total standing crop is categorized by growing seasons after burning. Redmann et al. (1993) reported total standing crop recovered to unburned levels 3 to 4 years after burning.

Return intervals of fires are an important consideration when including fire in the conservation of *Festuca*- and *Stipa-Agropyron*-dominated grasslands. Burning *Festuca*- and *Stipa-Agropyron* communities reduced or had no effect on current year standing crop. Although not definitive, our results also suggest that limited or excessive amounts of litter can hinder production in *Festuca*-dominated grasslands. Limiting litter accumulation by burning *Festuca* too frequently would limit production, as would burning infrequently and allowing large amounts (greater than about 350 g m^{-2}) of litter to accumulate. In comparison our findings suggest precipitation places greater controls on production than amounts of litter in *Stipa-Agropyron* communities.

Aside from the changes in current year standing crop, litter and total standing crop after burning, it is imperative that other conservation goals be considered for *Festuca*- and *Stipa-Agropyron*-dominated grasslands. Annual burning in these grass-

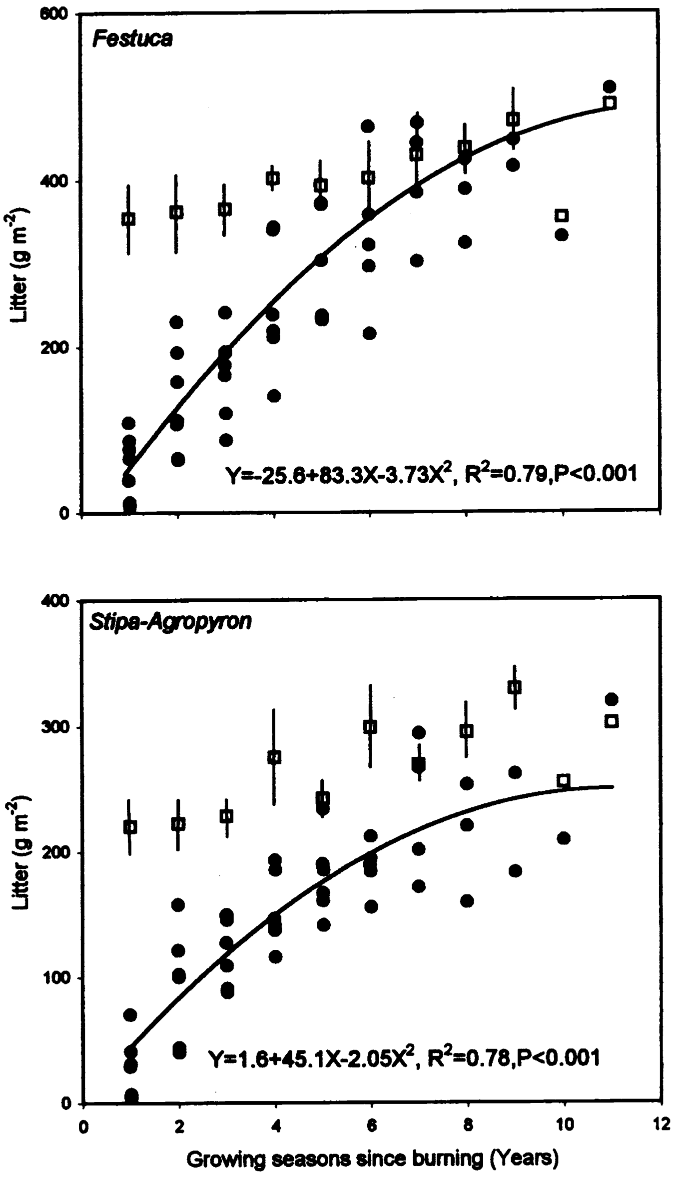

Fig. 3. Fitted regression lines and observed values for litter and growing seasons since burning in *Festuca*- and *Stipa-Agropyron*-dominated plant communities. Solid circles are observed litter after burning and open squares with vertical lines are means ± SE for the control.

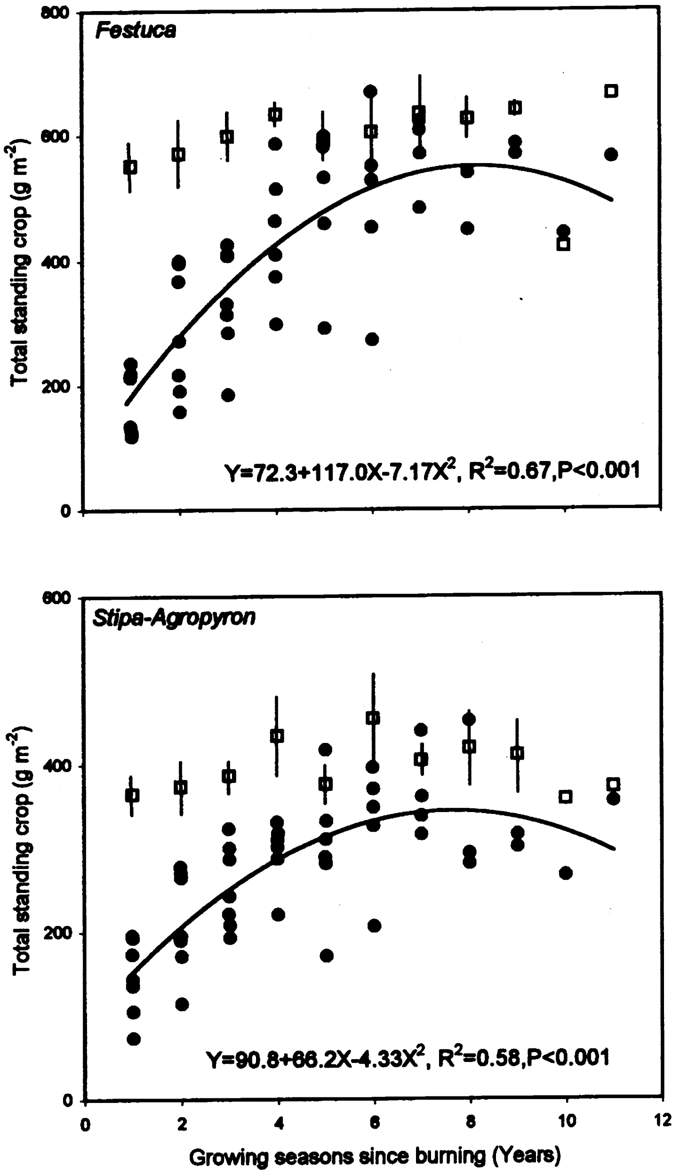

Fig. 4. Fitted regression lines and observed values for total standing crop versus growing seasons since burning in *Festuca*- and *Stipa-Agropyron*-dominated plant communities. Solid circles are total standing crop observed after burning and open squares with vertical lines are means ± SE for the control.

lands changes the structure in these grasslands by favoring species of warmer and drier conditions (Anderson and Bailey 1980). Furthermore Redmann (1991) argued that losses of nitrogen to volatilization by burning can exceed nitrogen inputs by 3- to 6-fold, and burning more frequently than every 4 years could cause a negative nitrogen balance in these grasslands.

Eighty-two percent of the native prairie in Saskatchewan has been cultivated for growing annual crops (Saskatchewan Agriculture and Food 1998), and about 5% of the prairie dominated by plains rough fescue remains (Grilz and Romo 1995). Prairie remnants such as Kernen Prairie are important habitats for many species of wildlife, and are especially valuable as developed agricultural and urban lands often surround these remnant prairies. For example, certain species of birds require grasslands that have recovered from burning while others are most abundant when plant communities are in various states of recovery after burning (Pylypec 1991, Madden et al. 1999, 2000). Conservation goals of grasslands may also require significant amounts of dead plant material to provide nesting cover and foraging sites for wildlife. Burning should be infrequent (11 years or longer) when maintenance of large amounts of litter or total standing crop are concerns in both *Festuca* and *Stipa-Agropyron* communities. Five- (Trottier 1985) to 10 (Wright and Bailey 1982) year return intervals have also been proposed for Fescue Prairie. Barrett (1997, 1999) estimated fire return intervals averaged about 10 to 26 years and ranged from 1 to 60 years in Fescue Prairie in the foothills of the Rocky Mountains in Montana. The actual frequencies of burning needed to achieve conservation goals must be adjusted for management objectives and prevailing conditions of the prairie remnant under consideration. In practice, conservationists should probably strive to maintain a mosaic of burned patches within remnants of *Festuca*- and *Stipa-Agropyron*-dominated grasslands, each in various states of recovery.

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J. Range Manage.
56: 646-653 November 2003

Nitrogen effects on seed germination and seedling growth

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Abstract

Recent evidence associates the persistence of invasive plant species with disturbance and fluctuations in distinct forms of mineral N in soils. We conducted soil and hydroponic experiments to investigate the influence of N form and availability on germination and seedling development of 2 invasive annual grasses, cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) and 6 perennial grasses, bluebunch wheatgrass (*Pseudoroegneria spicata*), crested wheatgrass (*Agropyron cristatum* x *A. desertorum*), Sand Hollow and Seaman's Gulch big squirreltail (*Elymus multisetus*), and Little Camas and Little Wood bottlebrush squirreltail (*E. elymoides* ssp. *brevifolius* and *E. elymoides* ssp. *elymoides*, respectively). Seeds were sown in soils with no soil additions, barley straw (1 mg kg^{-1}), NH_4^+ = 10 mg N kg^{-1}, NH_4^+ + I (nitrification inhibitor) = 10 mg N kg^{-1} + 37 ml nitrapyrin, or NO_3^- = 10 mg N kg^{-1} to evaluate cumulative germination percentage for 20 days in an incubator. For the hydroponic experiment, grass seedlings were exposed to distinct forms and uniform concentrations of mineral N to monitor root and shoot growth for 21 days. Treatments were no N added, NH_4^+ (1 mM), NO_3^- (1 mM), and NH_4NO_3 (0.5 mM). Treatments did not alter germination in the soil experiment. Lack of soil N effect on seed germination is attributed to the absence of seed dormancy in the populations of grasses we evaluated. Initial root length and overall shoot growth of grasses were greater in the NO_3^- than in the NH_4^+ treatment more frequently for perennial grasses. Root and shoot growth of medusahead and cheatgrass generally exceeded that of the other grasses except crested wheatgrass. However, relative decreases in root dry mass for the no N treatment were greater for the invasive annual grasses than the perennial grasses when compared to the N-addition treatments.

Resumen

Evidencia reciente asocia la persistencia de especies de plantas invasoras con el disturbio y las fluctuaciones de las distintas formas de N mineral de los suelos. Condujimos experimentos en suelo e hidroponía para investigar la influencia de la forma del N y su disponibilidad en la germinación y desarrollo de plántulas de 2 zacates anuales invasores "Cheatgrass" (*Bromus tectorum*) y "Medusahead" (*Taeniatherum caput-medusae*) y 6 zacates perennes "Bluebunch wheatgrass" (*Pseudoroegneria spicata*), "Crested wheatgrass" (*Agropyron cristatum* x *A. desertorum*), "Sand Hollow", "Seaman's Gulch big squirreltail" (*Elymus multisetus*), "Little Camas" y "Little Wood bottlebrush squirreltail" (*E. elymoides* ssp. *brevifolius* y *E. elymoides* ssp. *elymoides*, respectivamente). Las semillas fueron sembradas en suelos si adiciones de suelo, paja de cebada (1 mg kg^{-1}), NH_4^+ = 10 mg N kg^{-1}, NH_4^+ + I (inhibidor de nitrificación) = 10 mg N kg^{-1} + 37 ml nitrapirin o NO_3^- = 10 mg N kg^{-1} para evaluar el porcentaje acumulativo de germinación durante 20 días en una incubadora. En el experimento hidropónico las plántulas de zacate fueron expuestas a distintas formas y concentraciones uniformes de nitrógeno mineral para monitorear el crecimiento de raíz y tallo durante 21 días. Los tratamientos fueron: No adición de N, NH_4^+ (1 mM), NO_3^- (1 mM) y NH_4NO_3 (0.5 mM). Los tratamientos no alteraron la germinación en el experimento realizado con suelo, la falta de efecto del N del suelo en la germinación de la semilla se atribuye a la ausencia de dormancia de la semilla de las poblaciones de zacates que fueron evaluadas. La longitud de la raíz inicial y el crecimiento general del tallo de los zacates fue mayor en el tratamiento de NO_3^- que en de NH_4^+, esto se presentó más frecuentemente en los zacates perennes. El crecimiento de raíz y tallo en el "Medusahead"y "Cheatgrass"generalmente excedió el alcanzado por los otros zacates, excepto el "Crested wheatgrass". Sin embargo, las disminuciones relativas de la biomasa seca de la raíz en el tratamiento sin aplicación de N fue mayor para los zacates invasores que para los zacates perennes cuando se compararon con los tratamientos de adición de N.

Key Words: perennial grass, invasive annual grass, seedling establishment, nitrate, ammonium, root growth

Many shrub-steppe plant communities of the Intermountain West have been replaced by the invasive annual grasses cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski). Re-establishing perennial grasses by seeding semi-arid rangelands is challenging because these invasive annual grasses have higher reproductive potentials (Mack and Pyke 1983, Young 1992), more persistent seed banks (Hassan and West 1986, Humphrey and Schupp 2001), and higher growth rates (Arredondo et al. 1998) than most perennial grasses. Consequently, there is tremendous need to develop soil and seedbed treatments to improve germination, emergence, and early seedling growth of desirable perennial species.

Research was funded by USDA-ARS and USDA-CSREES Grant No. 97-38300-4892. We extend appreciation to Kevin Connors for his critical assistance in developing the design and attentive execution of the soil experiments. We also thank Justin Williams, Brandon Gordon, Jacqueline Adams, Tyler Sorensen, and Brandy Jones for assisting with seed and data collection. Drs. T. Svejcar and U. Choromanska provided helpful reviews on a previous draft of this manuscript.

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Manuscript accepted 2 Feb. 03.

Recent evidence strongly associates the persistence of invasive plant species and the loss of native species with disturbance and fluctuations in soil fertility (Huenneke et al. 1990, Burke and Grime 1996, Davis et al. 2000). The addition of mineral N to disturbed rangelands has been found to increase the relative abundance of cheatgrass, while reductions in N availability generally increased the relative abundance of perennial species (Paschke et al. 2000). Young et al. (1995, 1998) found seedling establishment of medusahead increased with NO_3^- fertilization, was unaffected by NH_4^+ fertilization, and decreased when mineral N was immobilized. These field experiments suggest that modifications in soil N availability and mineral N form may decrease establishment of invasive annual grasses. However, it is unclear whether these soil modifications will impact desirable perennial grasses frequently seeded in the Intermountain West.

The goal of our study was to evaluate the influence of N form and availability on germination and early seedling development of cheatgrass, medusahead, and 3 perennial grass species. With favorable precipitation, most seeds of cheatgrass and medusahead germinate the year they are produced, and seeds of the perennial grasses are typically non-dormant when utilized for seeding rangelands. We hypothesized that N availability and distinct forms of N would not alter percent germination or germination rate of these species when provided adequate moisture (Hypothesis I). Additionally, we hypothesized that early seedling growth of the invasive annuals, but not the perennials, would be greater when provided NO_3^- rather than NH_4^+ (Hypothesis II).

Materials and Methods

Plant Species

We collected cheatgrass (CG) and medusahead (MH) seed from populations located on southwest facing slopes (~ 1,450 m elev.) in Cache County, Ut. (41° 46' 07" N, 111° 47' 11" W for cheatgrass and 41° 32' 18" N, 111° 48" 00" W for medusahead). We refer to seed collected in summer 1997 as CG1 and MH1 and seed collected in summer 2000 as CG2 and MH2. We obtained seed for the following 6 perennial grasses: 'Goldar' bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), 'CD II' crested wheatgrass (*Agropyron cristatum* (L.) Gaertner x *A. desertorum* (Fisch. ex Link) Schultes), Sand Hollow (Jones et al. 1998) and Seaman's Gulch big squirreltail (*Elymus multisetus* [J.G. Smith] M.E. Jones), and Little Camas and Little Wood bottlebrush squirreltail (*E. elymoides* [Raf.] Swezey ssp. *brevifolius* and *E. elymoides* ssp. *elymoides,* respectively) from the USDA-ARS Forage and Range Research Laboratory in Logan, Ut. Seeds of bluebunch wheatgrass, Sand Hollow big squirreltail, crested wheatgrass, and the invasive annual grasses collected in 2000 (CG1 and MH2) were used in the soil germination experiment. All 10 grasses were used in the hydroponic experiment. Seeds of cheatgrass, medusahead, and squirreltail were de-awned prior to the experiments.

Soil Germination Experiment

The effects of mineral N form and availability on seed germination were evaluated in soil excavated from Dugway Proving Grounds (40° 14' 23" N, 112° 50' 47" W) in Tooele County, Ut. to a maximum depth of 60 cm. The top 2 cm of soil and litter were discarded to remove existing seeds on the soil surface. The soil was classified as coarse-loamy, mixed, calcareous, superactive, mesic Xeric Torriorhent and is a member of the Medburn Series (Trickler et al. 2000). The pH_{H2O} of the soil was 8.2, and cation exchange capacity (CEC) was 7-cmol kg^{-1} soil. Total soil carbon (C) (13 g kg^{-1}) and total soil N (1.0 g kg-1) were determined by direct combustion with a LECO CHN-1000 Autoanalyzer (LECO Corp., St. Joseph, Mich.)[1]. The gravimetric water contents at field capacity (–0.033 MPa) and permanent wilting point (–1.50 MPa) were 6.9 and 3.6%, respectively. The soil was passed through a 6-mm sieve to remove rocks and organic debris and then thoroughly mixed. Soil was placed in 30-liter plastic containers assigned to the following 5 soil treatments: 1) control = nothing added to soil, 2) straw = barley straw (1 mg kg^{-1} soil) ground to pass a 1-mm screen, 3) NH_4^+ = 10 mg N kg^{-1} soil added as $(NH_4)_2SO_4$, 4) NH_4^+ + I (nitrification inhibitor) = 10 mg N kg^{-1} soil added as $(NH_4)_2SO_4$ + 37 ml nitrapyrin (29% a.i., 2-chloro-6-(trichloromethyl) pyridine), and 5) NO_3^- = 10 mg N kg^{-1} soil added as $Ca(NO_3)_2$. Nitrapyrin inhibits the first nitrification step of bacterial NH_4^+ oxidation and stabilizes NH_4^+ in soils for about 60 days. The straw treatment was designed to decrease overall mineral N availability by promoting microbial immobilization of mineral N. The C:N ratio of the straw we used was 98 as measured with a LECO CHN-2000 Autoanalyzer (LECO Corp., St. Joseph, Mich.). Preliminary experiments indicated nearly all (> 95%) extractable soil mineral N was immobilized by the straw treatment within 5 days when at field capacity (6.9%). Thus, the straw treatment was watered to field capacity 5 days prior to the experiment, and the other 4 treatments were applied 1 day prior to the experiment with sufficient water to reach field capacity. Preliminary experiments indicated that treatment solutions were evenly distributed throughout soils within 24 hours.

The soil germination experiment was a completely randomized design with 5 treatments, 8 grasses, and 4 replications. The entire experiment was repeated 3 times on different dates. The 5 soil treatments were produced within plastic germination boxes (11 cm x 11 cm x 4 cm). To each box we added 250 g of soil (at field capacity) by shaking soil through 2 wire-mesh screens (2-mm), placed 100 grass seeds spaced 1-cm apart on the soil surface, and added 50 g of soil to cover seeds (~3 mm). Soil in each box was then lightly compressed with a wood block, and the soil surface dampened with de-ionized water to maintain soil dampness. Germination boxes were sealed with a lid and placed in a dark, temperature-controlled incubator held at 20° C for 20 days. Each box was evaluated daily and systematically relocated within the incubator. Germinated seeds (plumule emerged from soil surface) were removed with tweezers to minimize soil disturbances and resprayed with de-ionized to maintain soil dampness. Additionally, germination of each grass was evaluated by placing 100 seeds on blue blotter paper (Anchor Paper, St. Paul, Minn.) within seed boxes. Blotter paper germination was evaluated only once with each species replicated 4 times. Germination was evaluated for 20 days under the same incubator conditions as the soil experiment. De-ionized water was added when necessary to maintain visible wetness between the seeds and the blotter paper.

Soils of each treatment were analyzed at Day 10 for mineral N according to the methods described by Hart et al. (1994). Soils for N analysis were taken from an additional 8 replications of each treatment that were prepared with the first run of the experiment. These 8 additional treatment replications were seeded with crested

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[1] Mention of a trade name does not imply an endorsement or recommendation by USDA over similar products or companies not mentioned.

wheatgrass to provide an accurate estimate of soil NO_3^- and NH_4^+ at the midpoint of the experiment. A 10-g soil sample was taken from each seed box, homogenized, and extracted with 2 M KCl within 4 hours. Extracts were filtered through filter paper pre-leached with 2 M KCl and frozen until analyzed. Concentrations of NO_2^- + NO_3^- and NH_4^+ were analyzed colorimetrically with a flow injection autoanalyzer (Lachat Instruments, Milwaukee, Wis.) using standard procedures (Lachat 1989, 1990).

Hydroponic Experiment

The influence of distinct forms of mineral N on germination and subsequent seedling growth of the 2 invasive annual grasses and the 6 perennial grasses were evaluated in a hydroponic experiment. Because both NO_3^- and NH_4^+ forms are readily soluble in water, a hydroponic system was used to allow a direct comparison of mineral N forms independent of differences in nutrient mobility that could impact N uptake. Four aerated 15-liter tanks were filled with water and N-free modified 10% Hoagland's solution (trace elements and Fe at full strength). Holes in the lid of each tank accommodated the placement of 20-ml disposable beakers that rested at the surface of the hydroponic solution. These small beakers had a 16-mm diameter hole in the bottom that was covered by a large-mesh screen and contained 2 ml of agar (0.75%). In each beaker, 6 seeds of 1 of the grasses were placed on the agar surface with the seed crease facing down and the embryo towards the center. The N-free modified 10% Hoagland's solution was used to prepare nutrient agar with 4 N-form treatments. Treatments were control = no N added, NH_4^+ (1 mM), NO_3^- (1 mM), and NH_4NO_3 (0.5 mM = 1 mM N). The hydroponic tanks were kept indoors at room temperature. Photosynthetically active radiation (350 mmol m^{-2} sec^{-1}) was provided to plants for 16 hours per day to sustain vegetative growth. Radiation was provided with a combination lamp enclosure that had one 400 W metal halide lamp and one 600-W high-pressure sodium lamp (Sunlight Supply Inc., Vancouver, Wash.). The lamp continually moved lengthwise along a motorized light track to enhance uniformity of light distribution. The hydroponic experiment was a completely randomized design with 4 treatments, 10 grasses, and 3 replicates assigned to different hydroponic tanks.

All solutions were monitored and maintained at pH 6.1 either manually or with an automated pH controller in the case of the NH_4^+-N treatment. Nitrogen levels were monitored, and solutions were replaced periodically to maintain N concentrations within 20% of the initial levels. Germinated seeds were counted at Day 10, and maximum root and shoot length were measured at Day 10 and 21. We anticipated that rapid germination would equate to greater shoot and root growth during the experiment. All plants were harvested and oven dried (60° C) to constant weight to determine root and shoot dry mass on Day 21.

Statistical Procedures

All statistical analyses were performed with $\alpha = 0.05$. The effects of soil N treatment on germination of the 8 grasses and blotter paper germination were analyzed with PROC GLM (SAS 1999) and tested for significance of grass, N treatment, and the interactions. Treatment differences in the concentration of mineral soil N were analyzed with one-way ANOVA. All means were compared with Tukey's (HSD) test. Effects of the hydroponic treatments on germination and seedling growth of the 5 species were analyzed with a mixed ANOVA model for grass, soil treatment, and the interactions (Littell et al. 1996).

Results

Soil Germination Experiment

Soil treatments were effective at manipulating mineral-N form and availability in the germination boxes (Fig. 1). Soil NO_3^- concentration was 3.5 times greater in the NO_3^- treatment than any of the other treatments during the middle of the soil germination experiment. Soil concentrations of NH_4^+ in the NH_4^+ and NH_4^+ + I treatments were about 5 times greater than the control, straw, or NO_3^- treatment. Consequently, total mineral-N concentration (NO_3^- + NH_4^+) of the 3 N treatments did not differ more than 5%, and their average was 2.6 and 75 times greater than the control and straw treatments, respectively.

Cumulative germination percent differed significantly among the grasses as early as 3 days (Fig. 2), but neither soil treatment nor soil treatment x grass interactions significantly affected germination. Medusahead reached maximum percentage germination at Day 3, whereas the other grasses generally did not reach this point until Day 5. Bluebunch wheatgrass and Sand Hollow big squirreltail did not reach maximum percentage germination until Day 11, and cheatgrass seeds continued to germinate until Day 17. Cumulative percentage germination for medusahead and Little Camas bottlebrush squirreltail at

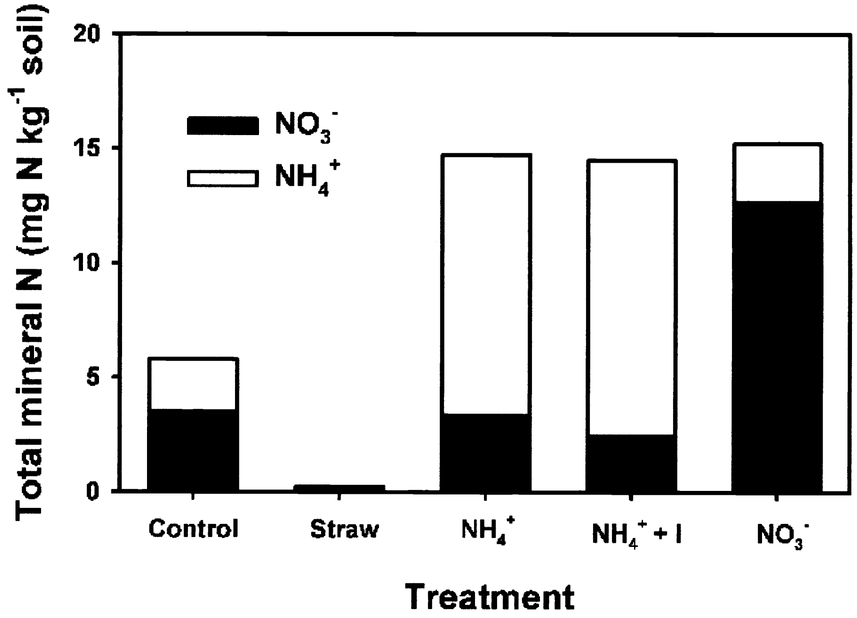

Fig. 1. Mean (n = 8) soil NO_3^- and NH_4^+ concentrations at Day 10 for 5 treatments evaluating the effects of mineral N forms and N availability on the germination of 2 invasive annual grasses and 6 perennial grasses.

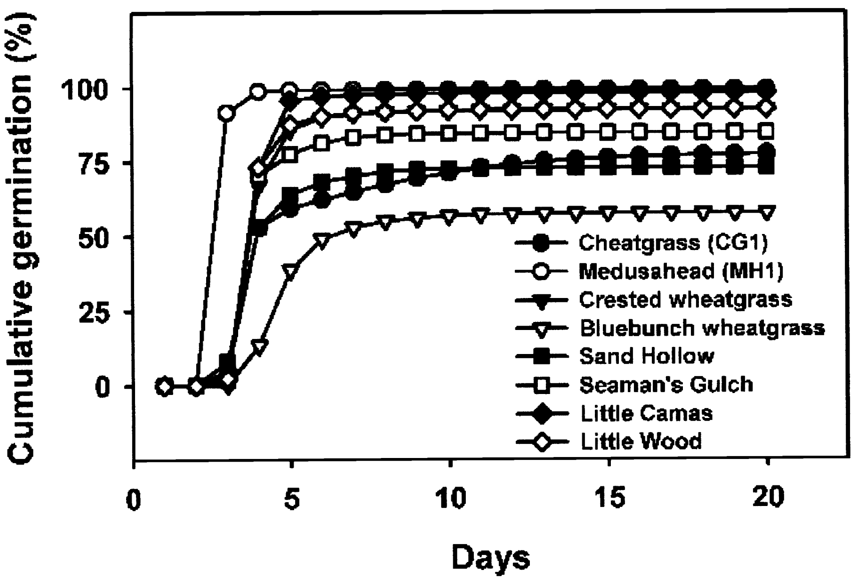

Fig. 2. Mean (n = 4) cumulative germination percentage of 2 invasive annual grasses and 6 perennial grasses exposed to 5 soil treatments that differed in mineral N forms and N availability for 20 days.

Day 20 was 99 and 98%, respectively, and was significantly greater than all other grasses. Crested wheatgrass and Little Wood bottlebrush squirreltail equally had the second highest cumulative percent germination of 92%, which significantly exceeded the remaining 4 grasses at Day 20. Bluebunch wheatgrass had the lowest cumulative germination percent (50%) at Day 20. Values for maximum cumulative germination in soil were comparable to values obtained on blotter paper without N additions (data not shown).

Hydroponic Experiment

Nitrogen treatment, grass, and treatment x grass interactions were significant for all seedling variables with the exception of treatment and the treatment x grass interaction for percentage germination. Germination of MH1 was almost 24% greater than MH2 (Table 1). Germination percentage was higher in the hydroponic system than in soil for CG1, bluebunch wheatgrass, and Sand Hollow big squirreltail.

Absolute shoot growth values of annual and perennial grasses were generally greater in the NO_3^- treatment than in the NH_4^+ treatment (Fig. 3), but significant differences were observed only for 5 of the native perennial grasses. Bluebunch wheatgrass and Seaman's Gulch and Little Wood squirreltails had significantly greater shoot dry mass in the NO_3^- treatment compared to the NH_4^+ treatment. Bluebunch wheatgrass was the only grass with significantly greater shoot length at Day 10 in the NO_3^- treatment compared to the NH_4^+ treatment. However, at Day 21, the 4 squirreltail populations were the only grasses to have significantly greater shoot length in the NO_3^- treatment than the NH_4^+ treatment. Cheatgrass was the only grass to have significantly greater shoot dry mass (CG1 and CG2) and shoot length (CG2) at Day 21 when grown in the NH_4NO_3 treatment compared to the NO_3^- treatment. Three of the squirreltails (Sand Hollow, Seaman's Gulch, and Little Camas) and medusahead (MH1) had significantly longer shoots than cheatgrass (CG1 and CG2) at Days 10 and 21 in the control treatment. Crested wheatgrass shoot lengths (at Days 10 and 21) in the control treatment were significantly less than 3 squirreltails (Sand Hollow, Seaman's Gulch, and Little Camas) at Day 10 and significantly less than all squirrelails and medusahead (MH1) at Day 21.

Root dry mass of MH1 in the control was significantly lower than all 3 N treatments (Fig. 4). The magnitude of difference in absolute root dry mass between the control and the NH_4NO_3 treatment was consistently lower for bluebunch wheatgrass and Sand Hollow and Seaman's Gulch big squirreltails compared to the invasive annual grasses and crested wheatgrass. For example, absolute root dry mass was 2- to 4-fold greater in the NH_4NO_3 treatment than in the control for cheatgrass (CG1 and CG2) and medusahead (MH2), while a response of this magnitude for perennial grasses was observed only in crested wheatgrass. Root dry mass was significantly greater in the NO_3^- treatment than in the NH_4^+ treatment for crested wheatgrass only.

Root length was generally greater in the N-free control treatment than in the 3 N treatments for most grasses, and this effect was more pronounced at Day 21 than Day 10 (Fig. 4). Medusahead (MH1 and MH2) root length at Days 10 and 21 in the control treatment exceeded ($P < 0.05$) that of perennial grasses with the exception of crested wheatgrass. Root lengths for both medusahead populations and 1 cheatgrass population (CG1) were significantly greater than all of the other grasses at Day 10 within the 3 N treatments. Roots of perennial grasses except bluebunch wheatgrass, and 1 medusahead population (MH1), were longer in the NO_3^- treatment than in the $NH_4NO_3^-$ treatment at Day 10 ($P < 0.05$). However, cheatgrass (CG2) was the only grass to have significantly longer roots in the NO_3^- treatment than the NH_4^- treatment by Day 21.

Shoot:root ratios were 2 to 2.5 fold greater in the 3 N treatments than the control for all grasses (Fig. 5). Cheatgrass (CG1 and CG2) had significantly lower shoot:root ratios than perennial grasses in the control. Similarly, the shoot:root ratio of medusahead was significantly less than Sand Hollow and Seaman's Gulch big squirreltails in the control treatment. Crested wheatgrass had a shoot:root ratio that was intermediate and similar to the other perennial grasses and the invasive annual grasses. Grasses other than cheatgrass, crested wheatgrass, and Little Camas bottlebrush squirreltail had greater shoot:root ratios in the NO_3^- than the NH_4^+ treatment ($P < 0.05$). In addition, absolute shoot:root ratios in the NO_3^-

Table 1. Mean (± 1 SE; n = 3) percentage germination based on appearance of root and shoot organs at 10 days after planting 6 seeds on agar contained in a culture assembly suspended over aerated nutrient solutions. Values followed by different letters indicate significant differences at P < 0.05.

Grass	Germination
	------(%)------
Cheatgrass (CG1)	84.7 ± 4.3 ab
Cheatgrass (CG2)	94.4 ± 2.4 a
Medusahead (MH1)	98.6 ± 1.4 a
Medusahead (MH2)	75.0 ± 4.6 b
Crested wheatgrass	90.3 ± 3.2 ab
Bluebunch wheatgrass	91.7 ± 3.2 a
Sand Hollow	86.1 ± 4.0 ab
Seaman's Gulch	84.7 ± 4.8 ab
Little Camas	98.6 ± 1.4 a
Little Wood	94.4 ± 2.4 a

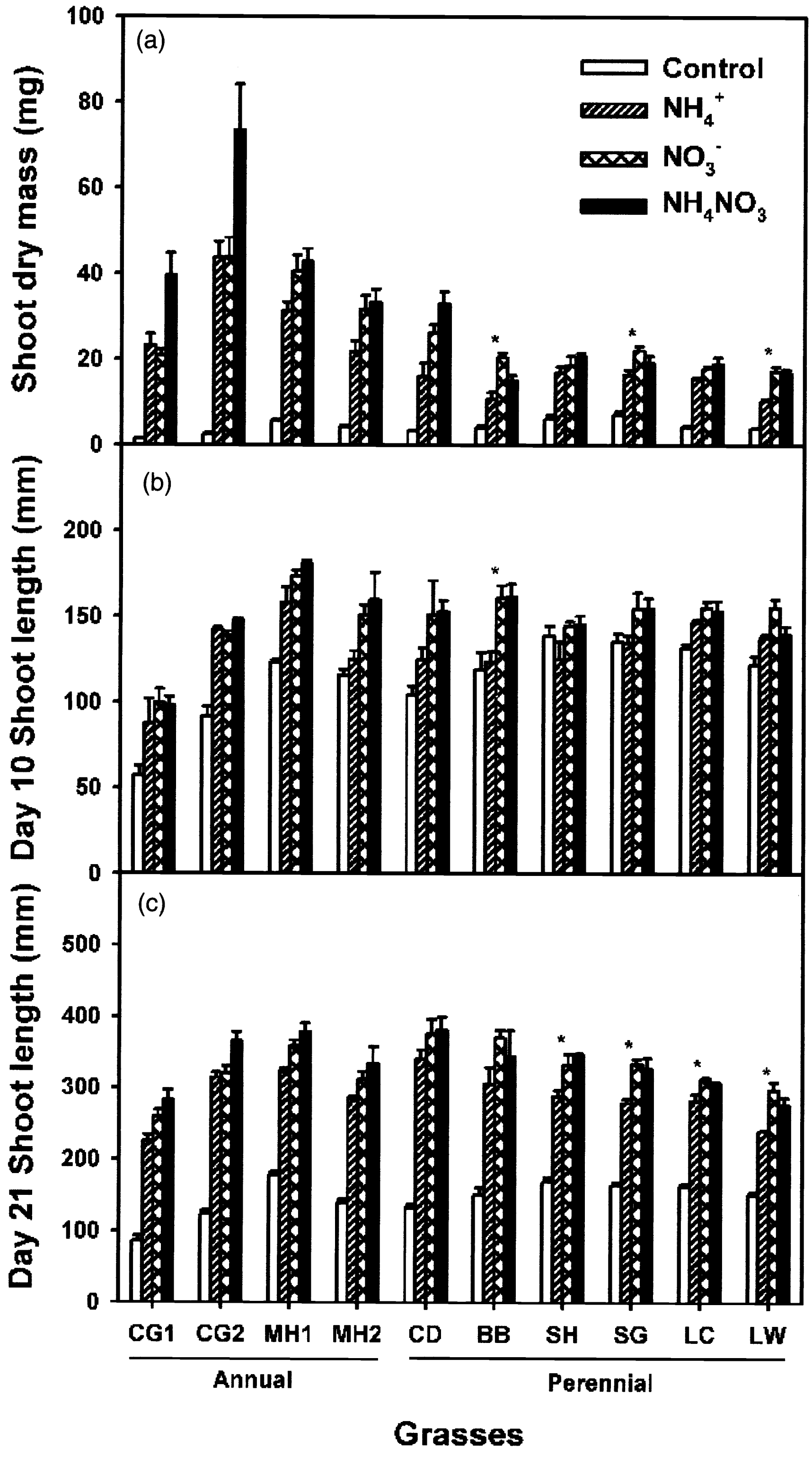

Fig. 3. Mean (± 1 SE; n = 3) shoot dry mass (a), shoot length at 10 days after planting (b), and shoot length at 21 days after planting (c) for populations of cheatgrass (CG1 and CG2), medusahead (MH1 and MH2), crested wheatgrass (CD), bluebunch wheatgrass (BB), and 4 squirreltails: Sandhollow (SH), Seaman's Gulch (SG), Little Camas (LC), and Little Wood (LW). Plants were grown in a hydroponic system to evaluate growth responses to mineral N forms and N availability. Asterisks above bars denote significant ($P < 0.05$) differences between the NH_4^+ and NO_3^- treatments.

treatment exceeded those in the NH_4NO_3 treatment for all grasses except cheatgrass and Little Camas bottlebrush squirreltail.

Discussion

The results of our germination experiments provide strong evidence that differences in N availability and forms of mineral N do not alter cumulative germination percentage of the populations of grasses we evaluated (Hypothesis I). Our hydroponic experiment demonstrated that seedling growth of annual and perennial grasses were generally greater when provided NO_3^- rather than NH_4^+. However, the perennial grasses generally showed a greater response to NO_3^- relative to NH_4^+ than the invasive annual grasses, which is contrary to Hypothesis II.

Soil Germination Experiment

Results from our germination experiment are similar to those of Goebel et al. (1988), who found medusahead germinated in one-third the time of bluebunch wheatgrass. Lower and slower germination percentage in bluebunch wheatgrass compared to the other grasses is likely one of the major factors that limit its ability to compete successfully with invasive annual grasses (Harris 1967). In contrast, more rapid and higher maximum germination percentage, as observed in crested wheatgrass and Little Camas and Little Wood squirreltails, may enable seedling emergence of these perennial grasses to coincide with the emergence of invasive annual grasses and to successfully compete with them (Forcella et al. 2000). Such advantages gained as seedlings are often retained as mature plants (Silverton and Dickie 1980, TeKrony and Egli 1991).

The results of our soil germination experiment agreed with those of other studies, demonstrating modifications in soil N do not alter seed germination of many grass and broad leaf weed species (Andrews et al. 1991, Riba et al. 2002). The lack of seed germination control by distinct forms of mineral N in our experiment may be associated with low levels of seed dormancy in the seeds evaluated. Varying levels of seed dormancy have been documented in medusahead and cheatgrass populations from disparate locations throughout the Great Basin, with populations from the relatively more arid regions generally having higher acquired dormancy (McKell et al. 1962, Meyer and Allen 1999). Non-dormant seeds of cheatgrass are known to germinate rapidly and completely regardless of genotype or envi-

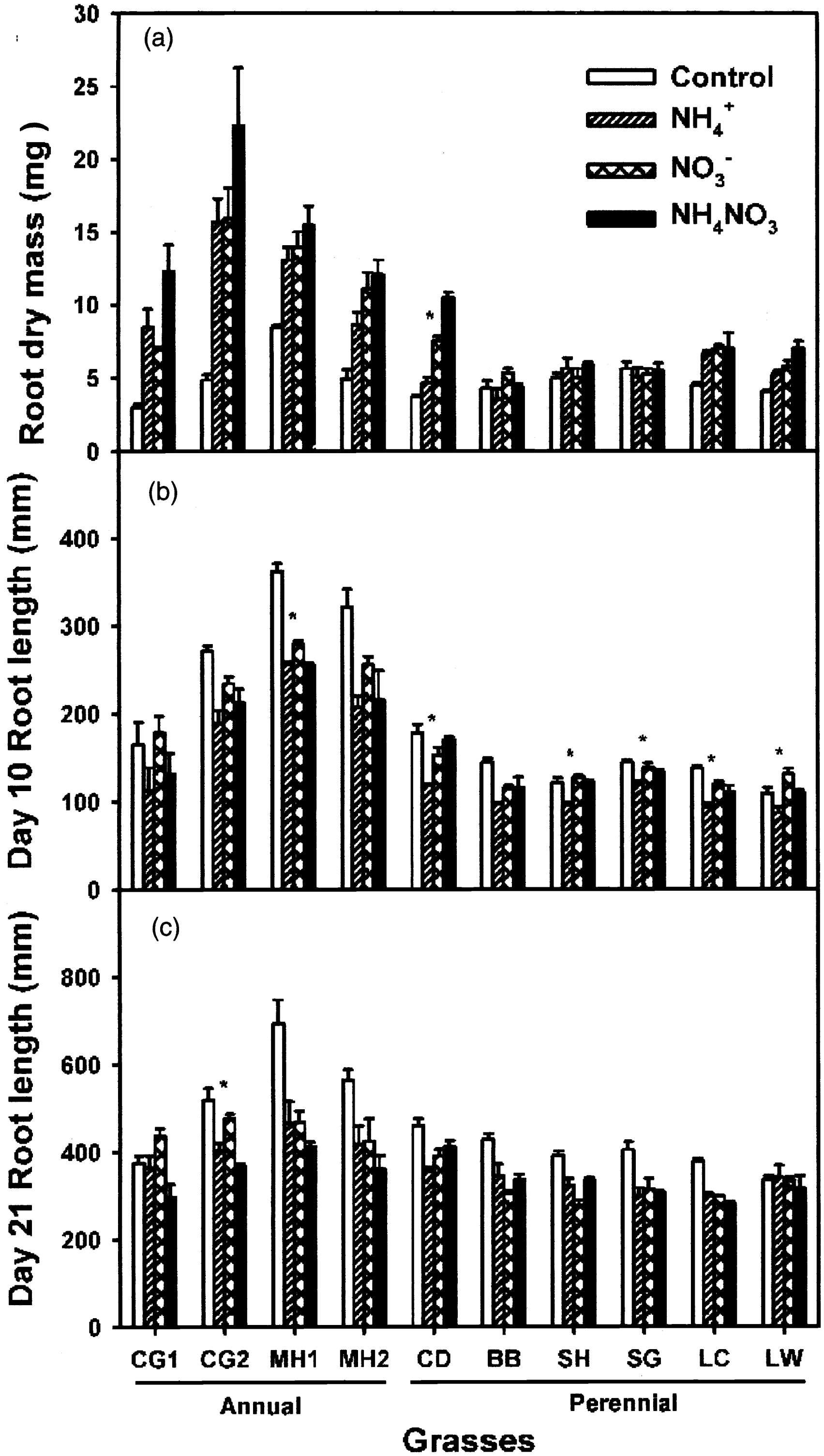

Fig. 4. Mean (± 1 SE; n = 3) root dry mass (a), root length at 10 days after planting (b), and root length at 21 days after planting (c) for populations of cheatgrass (CG1 and CG2), medusahead (MH1 and MH2), crested wheatgrass (CD), bluebunch wheatgrass (BB), and 4 squirreltails: Sandhollow (SH), Seaman's Gulch (SG), Little Camas (LC), and Little Wood (LW). Plants were grown in a hydroponic system to evaluate growth responses to mineral N forms and N availability. Asterisks above bars denote significant ($P < 0.05$) differences between the NH_4^+ and NO_3^- treatments.

ronmental factors (Allen and Meyer 2002). However, if seed water contents are not favorable for germination in the autumn following seed production, seeds of cheatgrass and medusahead may acquire dormancy (Hulbert 1955, Sharp et al. 1957, Young et al. 1969) and require specific environmental or chemical stimuli like NO_3^- to break dormancy (Evans and Young 1975, Hilton and Thomas 1986, Pons 1989, McIntyre et al. 1996).

Hydroponic Experiment

Initial root lengths at Day 10 and overall seedling shoot growth of perennial grasses responded more positively to NO_3^- relative to NH_4^+ than did invasive annual grasses. These results provide the principal justification for rejecting Hypothesis II. However, by Day 21, root lengths were similar in the NO_3^- and NH_4^+ treatments for all grasses except cheatgrass (CG2), suggesting distinct mineral forms produced merely a transient effect on root lengths. In contrast, the number of perennial grasses with significantly greater shoot lengths in the NO_3^- treatment than the NH_4^+ treatment increased between Day 10 and 21. Similarly, Glinski et al. (1990) found that root growth and root:shoot ratios of creeping bentgrass (*Agrostis palustris* Hudson) were higher when NO_3^- was the predominant form of mineral N. These responses may be associated with different carbon costs for N uptake and assimilation in perennial compared to invasive annual grasses (e.g., Anandacoomaraswamy et al. 2002), even though the carbon costs of assimilating NO_3^- are generally greater than NH_4^+ (Clarkson 1985). It is also possible that NH_4+ may have inhibited radicle elongation (Westwood and Foy 1999) and contributed to less root growth in the NH_4^+ than the NO_3^- treatment. The ecological significance of perennial grasses being more responsive than annual grasses to the NO_3^- vs. NH_4^+ comparison is unknown, but further identification of the underlying mechanisms responsible for these responses may reveal critical insights into competitive interactions between these 2 groups of grasses.

Early seedling root and shoot growth must be tailored to take advantage of soil N that rapidly becomes available to plants following nutrient flushes associated with precipitation and soil disturbance events (Chapin 1980, Fisher et al. 1987, Burke 1989). Our results suggest invasive annual grasses may be more capable to take advantage of ephemeral pulses of N in rangeland soils than perennial grasses.

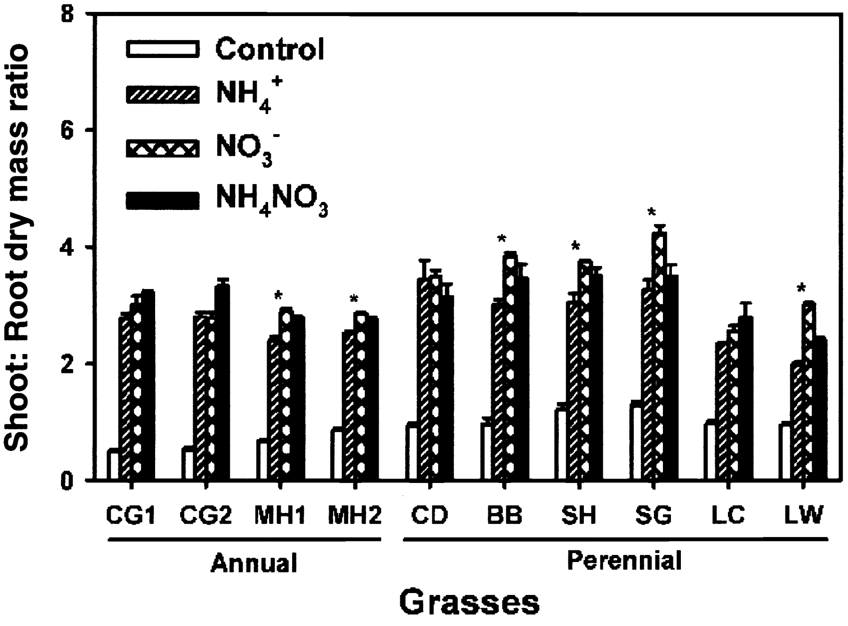

Fig. 5. Mean (± 1 SE; n = 3) shoot:root dry mass for populations of cheatgrass (CG1 and CG2), medusahead (MH1 and MH2), crested wheatgrass (CD), bluebunch wheatgrass (BB), and 4 squirreltails: Sandhollow (SH), Seaman's Gulch (SG), Little Camas (LC), and Little Wood (LW). Plants were grown in a hydroponic system to evaluate growth responses to mineral N forms and N availability. Asterisks above bars denote significant ($P < 0.05$) differences between the NH_4^+ and NO_3^- treatments.

Root and shoot growth of medusahead seedlings exceeded all grasses except crested wheatgrass regardless of treatment (Hironaka 1961, Harris 1977). Our experiment showed medusahead and cheatgrass generally had greater root dry mass and more rapid development of root length (at Day 10) than the other grasses except crested wheatgrass. Similarly, Harris and Wilson (1970) found roots of crested wheatgrass grew faster than bluebunch wheatgrass and almost as fast as cheatgrass and medusahead roots. Our observation that crested wheatgrass root responses were intermediate to the annual and native perennial grasses confirm previous reports that crested wheatgrass has greater early-spring root growth and root proliferation in fertilized soil microsites (Eissenstat and Caldwell 1988, Caldwell et al. 1991) and earlier seedling emergence (Pyke 1990) than the native perennial, bluebunch wheatgrass. Collectively, these data explain mechanisms whereby faster-growing annual grasses (Arredondo et al. 1998) with high NO_3^- uptake and greater N productivity (i.e., biomass produced per unit of N) (Poorter et al. 1990, Garnier and Vancaeyzeele 1994) reduce the success of seeded perennial grasses on semiarid rangelands (Hironaka 1961).

Comparisons of the N treatments with the N-free control treatment showed that root dry mass of the invasive annual grasses and crested wheatgrass exhibited a greater percentage reduction in low compared to high N conditions than the native perennial grasses. These results agree with the general observation that low nutrient availability induces greater growth reductions in species with high potential growth rates (annuals) than those with low potential growth rates (perennials) (Shipley and Keddy 1988, Muller and Garnier 1990). Although all grasses in our experiment generally increased mass partitioning to roots in response to low N, shoot:root ratios of perennial grasses were generally greater than the invasive annual grasses in low N. Consequently, if low-N conditions are relatively less detrimental to perennial grasses than invasive annual grasses, there may be potential to develop management scenarios to specifically improve seedling establishment of perennial grasses on rangelands by reducing N availability (Paschke et al. 2000).

Our results showed specific seedling traits were modified by distinct forms of mineral N and confirm previous reports that rapid seedling establishment of invasive annual grasses is associated with the ability to exploit nutrients and rapidly produce more root (Harris 1967) and shoot mass than perennial grasses (Svejcar 1990). Our observation of lower percentage reduction in seedling growth in low compared to high soil N availability in the perennial grasses than the invasive annual grasses suggests that reducing mineral N may improve the relative establishment of perennial grasses by impeding growth of invasive annuals (Borman et al. 1991).

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J. Range Manage.
56: 654-659 November 2003

Carbon isotope discrimination and yield in 14 cool-season grasses

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Abstract

Selection for carbon isotope discrimination (Δ) has potential for improving water-use efficiency in cool-season grasses. An understanding of how Δ is affected by differential water application and its association with dry mater yield may be helpful in identifying the best cool-season grass species for breeding and improvement, and may assist in designing selection and breeding procedures for improving cool-season grasses. We designed a study to evaluate the response of Δ and dry matter yield to a gradient of water application in 14 cool-season, perennial grasses. The grasses were established in a rainout shelter facility equipped with a line-source irrigation system to study the: i) trends in dry matter yield across 6 water levels (WL-1 through 6, ranging from 981 to 64 mm water applied) and Δ across 3 water levels (WL-1, 3, and 5), ii) grass x water level interactions for these traits, and iii) relationship between dry matter yield and Δ in these grasses across a 2-year period. When averaged across years, the grasses differed significantly for Δ at the highest (WL-1) and lowest (WL-5) water levels, but not at WL-3. Reductions in Δ were strongly linear from WL-1 to WL-5, and although some inconsistencies were evident, the trend was similar for all grasses. Grasses differed significantly for dry matter yield at each of the water levels. Although the change in dry matter yield was mostly linear across water levels, the trend was not consistent among the grasses. In general, Δ was not closely associated with dry matter yield; however, some exceptions with high dry matter yield and high Δ were evident. This lack of close association between dry matter yield and Δ in these 14 grasses suggests that breeding efforts to improve these grasses should involve simultaneous selection for dry matter yield and Δ.

Key Words: water-use efficiency, dry matter yield, line-source sprinkler system, rainout shelter, forage

The mechanisms plants use to respond to drought and the various screening methods that have been used to improve drought responses of forage grasses were reviewed by Asay and Johnson (1983) and Johnson and Asay (1993). Ideally, forage grasses should produce large amounts of high quality forage and at the same time make efficient use of limited water resources (water-use efficiency, amount of carbon gained per unit of water transpired). Because of the overriding influence of limited water on plant growth, screening procedures used in breeding programs for rangeland and pasture plants in the western U.S. must be able to identify breeding lines that combine superior productivity with high water-use efficiency.

Finding appropriate screening techniques to assess water-use efficiency has proven extremely challenging, and a lack of effec-

Resumen

La selección por medio de la discriminación del isótopo de carbón (Δ) tiene el potencial para mejorar la eficiencia del uso del agua en zacates de estación fría. Un entendimiento de cómo Δ es afectado por la aplicación diferencial de agua y su asociación con el rendimiento de materia seca puede ser útil en identificar las mejores especies de estación fría para el mejoramiento genético y puede ayudar en diseñar procedimientos de selección y mejoramiento genético de estos zacates. Diseñamos un estudio para evaluar la respuesta de Δ y el rendimiento de materia seca a un gradiente de aplicación de agua en 14 zacates perennes de estación fría. Los zacates se establecieron en una instalación equipada con protector contra lluvia y con un sistema de irrigación de línea para estudiar: i) las tendencias en el rendimiento de material seca a través de 6 niveles de agua (WL-1 al 6, fluctuando de 981 a 64 mm de agua aplicada) y el Δ en tres niveles de agua (WL-1, 3, y 5), ii) interacciones entre zacate x nivel de agua para estas características y iii) la relación entre la materia seca y Δ en estos zacates en un período de 2 años. Cuando se promedio a través de los años, los zacates defirieron significativamente respecto a Δ en el nivel más alto (WL-1) y más bajo (WL-5) de agua, pero no hubo diferencia en el nivel WL-3. Las reducciones en Δ fueron lineales de WL-1 a WL-5, y aunque algunas inconsistencias fueron evidentes, la tendencia fue similar para todos los zacates. Las especies de zacate difirieron significativamente en cuanto a rendimiento de materia seca en cada uno de los niveles de agua. Aunque el cambio en la materia seca fue principalmente lineal a través de los niveles de agua, la tendencia no fue consistente entre las especies. En general, Δ no estuvo estrechamente correlacionado con el rendimiento de material seca, sin embargo, algunas excepciones con alta material seca y alto Δ fueron evidentes. Esta falta de una asociación estrecha entre el rendimiento de materia seca y _ en estos 14 zacates sugiere que los esfuerzos de mejoramiento genético para mejoralos debe involucrar la selección simultanea para el rendimiento de materia seca y Δ.

We express our appreciation to Kevin Connors for his skilled technical assistance during all phases of this research. Published as Journal Paper No. 7417 of the Utah Agricultural Experiment Station at Utah State University, Logan, Ut. 84322-4810.

Manuscript accepted 16 Jan. 2003.

tive screening procedures has impeded progress in evaluating plants for water-use efficiency. Although direct measurements of aboveground dry matter can be routinely assessed in field evaluations, accurate determinations of root dry mass and the amount of water transpired for each plant, which are required to calculate water-use efficiency, are impractical to obtain in most breeding programs. These challenges are compounded because of the many breeding lines that must be evaluated in typical plant improvement programs. In addition, measurements of transpiration rate, photosynthetic activity, and other traits associated with plant gas exchange or water relations represent instantaneous characterizations that may not reflect integrated responses across the multiple stages of plant development.

Farquhar et al. (1982) developed the theoretical basis for the relationship between carbon isotope discrimination (Δ) and leaf intercellular CO_2 concentration, which is associated with water-use efficiency. This theory suggests a negative association between Δ and water-use efficiency, which was first documented in wheat (*Triticum aestivum* L.) (Farquhar and Richards 1984, Condon et al. 1990). Since then, a negative relationship between Δ and water-use efficiency has been reported in a wide range of C_3 species (Brugnoli and Farquhar 2000), which includes the following cool-season grasses: crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schultes) (Read et al. 1991, Johnson et al. 1990); Altai wildrye (*Leymus angustus* (Trin.) Pilger) (Johnson et al. 1990); and orchardgrass (*Dactylis glomerata* L.), tall fescue (*Festuca arundinaceae* Schreb.), and perennial ryegrass *(Lolium perenne* L.) (Johnson and Bassett 1991). Based on theory and these documented relationships, Δ has been suggested as a means to improve water-use efficiency in C_3 crop species (Farquhar and Richards 1984) and in perennial, cool-season grasses (Johnson et al. 1990, Johnson and Bassett 1991, Asay et al. 1998). Because C is continually being assimilated through photosynthesis, Δ offers potential in integrating water-use efficiency responses across the growing season, which suggests that Δ may be more useful than most instantaneous physiological measurements for selection. Research related to Δ and plant breeding was reviewed by Hall et al. (1994).

The present study was designed to determine the response of Δ and dry matter yield to a gradient of water application in 14 perennial, cool-season forage grasses; examine the grass x water level interaction for Δ and dry matter yield; and evaluate the relationship of Δ to dry matter yield in these grasses. Establishing these relationships in a broader spectrum of cool-season grasses may contribute to a better understanding of the interaction between Δ and dry matter as affected by water. They also may be helpful in identifying the best cool-season grass species for breeding and improvement, and assist in designing selection and breeding procedures for improving water-use efficiency and dry matter yield in a broader scope of grass species and hybrids.

Materials and Methods

Plant Materials

The following 14 experimental breeding lines and cultivars of important cool-season, perennial grasses were included in the study: 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn. x *A. desertorum*; a breeding line of hexaploid (2n = 6x = 42) crested wheatgrass *(A. cristatum*); a breeding line (designated AI Hybrid) and 'Greenar' intermediate wheatgrass *[Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey]; 'Alkar' tall wheatgrass [*T. ponticum* (Podp.) Barkworth & D. R. Dewey]; 'Prairieland' Altai wildrye; a breeding line of *Leymus karelinii* (Turcz) Tzvelev; 'Magnar' Great Basin wildrye [*L. cinereus* (Scribn. & Merr.) A. Löve]; a breeding line of a trihybrid involving Great Basin wildrye, Altai wildrye, and mammoth wildrye [*L. racemosus* (Lam.) Tzvelev] designated as *Leymus* hybrid; a natural hybrid between bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] and crested wheatgrass designated as bluebunch wheatgrass hybrid; the cultivar 'NewHy' and a breeding line (RS-H) of the RS hybrid (*Elymus hoffmannii* Jensen & Asay); 'Manchar' smooth bromegrass (*Bromus inermis* Leyss); and 'Kay' orchardgrass. These various breeding lines and cultivars will be referred to hereafter as grasses.

Experimental Design

The study was conducted in a rainout shelter (10-m by 47-m plot area) modified after Upchurch et al. (1983), located at the Utah State University Evans Experimental Farm, approximately 2 km south of Logan, Utah (41° 45' N, 111° 48' W, 1,350 m above sea level). Soil at the study site is a Nibley silty clay loam series (fine, mixed, mesic Aquic Argiustoll). Plots of the individual grasses were established perpendicular to a line-source sprinkler in 3 rows of 14 plants with each plant being 30-cm away from its 4 neighboring plants. Single plants on the end of each row were designated as border plants. The remaining 36 plants (3 rows x 12 plants) were divided into 6 water levels, each consisting of 6 plants (3 rows x 2 plants). Plots receiving the most irrigation (WL-1) were located adjacent to the irrigation pipe, and plots receiving the least irrigation (WL-6) were the most distant from the irrigation pipe. The experiment was arranged as a modified split-plot design with the 14 grasses as whole plots and the 6 water levels as subplots. Whole plots were randomized in 4 blocks (replications), 2 on each side of the line-source irrigation pipe. The rainout shelter closed to cover the plots during most periods of precipitation and remained open at all other times. As a result, water received by the plots was restricted to that applied by the line-source irrigation system, except for some snow that was allowed to fall on the plot area during the winter.

Grass seeds were germinated in blotter trays, germinating seeds were transplanted into super-cell plastic cone-tainers (22 cm deep, 4 cm diam.) that contained 3:1 soil/peat (different than the soil in the rainout shelter), and plants were placed in a greenhouse. Seedlings were transplanted into field plots on 19 September 1991, and plots were watered uniformly as needed during that autumn for establishment. Irrigation treatments were initiated the first week of May and continued through October during 1992 and 1993 to establish the water gradient and during the following 2 years of data collection. Water application received in the study plots was measured with plastic rain gauges placed in each of the 6 water application treatments in each of the 4 replications of the experiment. Average amounts of water received by the 6 plots from May through October in 1994 and 1995 were 981, 916, 733, 465, 155, and 64 mm for WL-1 through WL-6, respectively. Individual water application amounts for 1994 were 846, 801, 640, 369, 156, and 96 mm for WL-1 through WL-6, respectively. Corresponding amounts in 1995 were 1,116, 1,030, 825, 560, 153, and 32 mm, respectively. Amounts of water application differed between the 2 years because of differing evapotranspiration demands and the associated amounts of water required to maintain the gradient of plant growth from the highest to the lowest water application levels. All plots received

85 kg N, P, and K ha^{-1} during mid-winter when the soil was frozen.

Data Collection

Plots were harvested at an 8-cm stubble height on 13–14 July during 1994 and 1995, which was after all grasses had flowered. An 8-cm stubble height was used because this represents an average height for cutting and/or grazing for the wide range of grasses evaluated in our study. A second harvest was made on 8–9 November in 1994 and 14–15 November in 1995. Dry matter yield (expressed as Mg ha^{-1}) was determined for the 2 harvest dates and 6 water levels in each year of data collection by drying the clipped forage at 60° C to a constant weight. For determinations of Δ, flag leaves were sampled from each plant at the first harvest of each year of data collection for WL-1, WL-3, and WL-5. The number of flag leaves harvested for each species within each water level varied from about 12 to 60 leaves because of the variation in flag leaf mass among the 14 grasses at their respective water levels. A minimum of 1 gram of ground, dried leaf material was required for the determination of Δ. Leaf samples were dried in a forced-air oven at 60° C and ground to pass through a 0.7-mm mesh screen and then combusted in a C and N analyzer (Carlo Erba NA-1500; Fisons Instruments, Valencia, California). The CO_2 and N_2 gases were separated at 50° C on a chromatographic column monitored by a thermal conductivity detector, and each peak was integrated for determination of percent N and C. The CO_2 gas was then transferred into a trapping system, cryogenically purified, and analyzed for $\delta^{13}C$ ($^{13}C/^{12}C$ ratio relative to that of the Pee Dee belemnite (PDB) standard) using an isotope ratioing mass spectrometer (SIRA 10; Fisons Instruments). Precision for $\delta^{13}C$ was better than 0.1‰ (per mil). Standards 21 and 22 (NIST) were used routinely to verify values of the working standards. The $\delta^{13}C$ values were converted to Δ as described by Farquhar et al. (1989), assuming that the $\delta^{13}C$ of air on the site was –8‰ on the PDB scale (Mook et al. 1983).

Statistical Analysis

Total dry matter yield and Δ were analyzed within and across grasses and years using the GLM procedure (SAS Institute Inc. 1999). Because the line-source sprinkler system does not allow water levels to be randomized within grasses, mean squares for grass, water level, and the grass x water level interaction were tested with their first-order interactions with replications. Statistical analyses were made at 6 water levels for dry matter yield and at 3 water levels for Δ. Data from individual years were treated as repeated measures in the analyses of data combined across years. Mean separations were made on the basis of the Fisher's protected least significant difference (LSD) at the 0.05 level of probability. Linear, quadratic, and cubic trends of dry matter yield and Δ across water level were determined for each grass using orthogonal polynomials with unequal intervals (Gomez and Gomez 1984). The slopes of linear regressions were also computed within each grass across water levels. The amount of water received at each water level was used in the computation of regression slopes and the coefficients used in the analyses of linear trends using orthogonal polynomials. This was done because the water applied was not linear across water levels.

Results

Carbon Isotope Discrimination

Grasses differed significantly ($P < 0.01$) for carbon isotope discrimination (Δ) in the analyses of data combined across the 3 water levels for each year and also when data were analyzed across years (Table 1). In the analysis of Δ values within water levels, grasses differed significantly ($P < 0.01$) at WL-1 and WL-5 in 1994, at WL-1 ($P < 0.01$) and WL-3 ($P < 0.05$) in 1995, and at WL-1 and WL-5 in the analysis combined across years. The variation among grasses as indicated by the range and standard deviation (SD) in Δ values was greatest at the driest water level, WL-5 (Table 2). When combined across years, the range and SD among Δ values were 1.8 and 0.56‰, respectively, for WL-5, which received an average of 155 mm of water from May through October. Corresponding values for the range and SD of Δ were 1.3 and 0.4‰ for WL-1 (981 mm water applied) and 0.9 and 0.29‰ for WL-3 (733 mm water applied), respectively. The mean slope (rate of change or b value) of the regression between Δ and water levels across all the grasses was 0.27‰ dm^{-1} water applied. Essentially all (99%) of the differences due to water level were associated with linear effects, as determined by orthogonal contrasts. The mean Δ values were 20.0‰ for WL-1, 19.6‰ for WL-3, and 17.8‰ for WL-5.

The grass x water level interaction (G x WL) for Δ was not significant in either year (Table 1), indicating that the grasses were responding in a similar manner to changes in water levels. Although the consistency across water levels is generally supported by the uniformity of the regression slopes (b values) for the individual grasses across water levels, some divergence was apparent (Table 2). The regression slopes were relatively consistent among the grasses except for the hexaploid crested wheatgrass strain (b = 0.42) and *Leymus karelinii* (b = 0.18) (Table 2). The decrease in Δ values was considerably greater with reduced water for hexaploid crested wheatgrass than the other

Table 1. Mean squares from ANOVA for carbon isotope discrimination (Δ) of 14 perennial, cool-season grasses at 3 water levels (WL) and combined across water levels, for each year separately and combined across 2 years.

		Carbon isotope discrimination (Δ)			
Source	df	WL-1	WL-3	WL-5	Combined
		------------------------------(‰)------------------------------			
1994					
Grass	13	0.88**	0.73	1.47**	2.31**
Water level (WL)	2	-----	-----	----	51.77**
Grass x WL	26	----	-----	-----	0.39
1995					
Grass	13	0.71**	0.58*	1.58	1.92**
Water level (WL)	2	-----	-----	-----	98.95**
Grass x WL	26	-----	-----	-----	0.47
Combined					
Grass	13	1.27**	0.67	2.55**	3.30**
Water level (WL)	2	-----	-----	-----	142.68**
Grass x WL	26	-----	-----	-----	0.59
Year	1	88.70**	102.05**	34.87**	208.31*
Grass x Year	13	0.32	0.64*	0.41	0.74**
WL x Year	2	-----	-----	-----	4.21**
Grass x WL x Year	26	-----	-----	-----	0.27

*,**Significant at 0.05 and 0.01 probability levels, respectively.

Table 2. Means and trends in carbon isotope discrimination (Δ) and total dry matter yield of 14 perennial, cool-season grasses at individual water levels (WL), combined across 2 years. Total dry matter yield was determined from combined individual harvests in July and November of 1994 and 1995 (n = 8).

	Δ					Dry matter yield				
	WL-1	WL-3	WL-5	b[1]	Lin.[2]	WL-1	WL-3	WL-5	b	Lin
	(‰)				(%)	(Mg ha^{-1})				(%)
Hycrest crested WG[3]	20.7	20.0	18.8	0.22	99	8.05	7.29	5.55	0.34	9
Hexaploid crested WG	20.5	19.4	17.0	0.42	100	5.54	3.14	2.23	0.35	82
AI intermediate WG	19.9	19.6	17.7	0.28	97	9.62	7.59	4.68	0.70	94
Greenar intermediate WG	20.2	19.8	18.2	0.25	99	9.45	7.76	5.10	0.61	93
Alkar tall WG	20.2	20.0	18.4	0.23	96	13.18	11.03	5.02	0.95	92
Prairieland Altai wildrye	20.5	19.6	18.1	0.29	100	6.37	7.10	4.14	0.42	87
Leymus karelinii	20.1	20.0	18.7	0.18	96	7.37	5.61	3.41	0.53	91
Magnar Basin wildrye	19.4	19.2	17.3	0.27	96	3.82	2.90	4.24	0.14	19
Leymus hybrid	19.7	19.6	17.6	0.27	95	10.34	7.45	4.27	0.78	96
Bluebunch WG hybrid	19.9	19.4	17.1	0.35	98	5.29	3.78	3.67	0.29	75
NewHy RS hybrid	19.7	19.5	17.5	0.27	95	6.19	6.03	3.12	0.58	86
RS-H RS hybrid	19.7	19.5	17.8	0.24	96	7.61	6.25	2.81	0.69	93
Manchar smooth brome	19.4	19.1	17.5	0.24	99	10.21	7.97	4.55	0.89	94
Kay orchardgrass	19.8	19.3	17.7	0.27	100	6.92	5.79	0.58	0.79	99
Mean	20.0	19.6	17.8	0.27	99	7.85	6.41	3.80	0.58	97
LSD$_{(0.05)}$	0.4	ns	0.7			1.43	1.19	1.09		
SD[4]	0.40	0.29	0.56			2.48	2.16	1.32		

[1] b = regression coefficient of Δ and dry matter yield of entries across WL. Although only 3 WL are reported here, 6 WL were used in determining the regression relationship. Values for WL (independent variable) expressed as dm of water received by plots.

[2] Lin. = Percent of WL sums of squares due to linear effects, based on orthogonal polynomials with unequal spacings.

[3] WG = wheatgrass

[4] SD = Standard deviation among entry means at each WL

grasses in our study, whereas those for *L. karelinii* exhibited the smallest change with decreasing water application. Within the different grasses, 95 to 100% of the variation due to water level was associated with linear effects. Some inconsistency in Δ across water levels is also indicated in the correlation matrix (Table 3). Although the correlations (r) among mean Δ values for the different water levels were significant ($P < 0.01$) between WL-1 and WL-3 ($r = 0.67$) and between WL-3 and WL-5 ($r = 0.88$), the r value between WL-1 and WL-5 was not significant ($P > 0.05$).

Dry Matter Yield

Grasses differed significantly ($P < 0.01$) for dry matter yield at all water levels in the analyses within years and in the analysis combined across years (Table 4). Relative differences among grasses were not consistent across water levels as indicated by the highly significant ($P < 0.01$) grass x water level interactions (G x WL) (Table 4). The correlation between WL-1 and WL-3 was positive and significant ($r = 0.92$, $P < 0.01$) (Table 3). Dry matter yield increased from WL-5 to WL-1 in a significant and near linear manner (Table 2). The mean rate of change, as indicated by the regression slope (b value) of dry matter yield with water application, was 0.58 Mg ha^{-1} of dry matter cm^{-1} of water applied. In addition, 97% of the variation due to water levels was associated with linear effects in the analysis of data combined across grasses and years. Considerable variation was found among b values indicating that dry matter yield of the grasses declined at different rates. For example, the b value for the cultivar Alkar tall wheatgrass was 0.95 and for Manchar was 0.89, indicating sharp declines of dry matter yield with decreasing water. In contrast dry matter yield for Magnar Basin wildrye was only 0.14, indicating a relatively uniform performance across water levels, but with a low dry matter yield at high available water (WL-1). These differences in response of grasses to water application were also a major factor contributing to the significant grass x water level interaction for dry matter yield.

Relationship between Dry Matter Yield and Δ

There was a consistently positive, but relatively low, correlation between carbon isotope discrimination (Δ) and dry matter yield (Table 3). The r values between the 2 traits were 0.05 for WL-1, 0.54 ($P < 0.05$) for WL-3, and 0.41 for WL-5. The correlation between Δ at WL-5 and dry matter yield at WL-3 also was significant ($r = 0.60$, $P < 0.05$). Although these general associations across all grasses were not strong, some exceptions were evident. For example, Δ for Hycrest crested wheatgrass was significantly greater than Δ for the hexaploid crested wheatgrass at the driest water level (WL-5). However, Hycrest produced significantly more dry matter than the hexaploid crested wheatgrass at WL-5 and the other 2 levels as well. A similar relationship was observed for Hycrest and the bluebunch wheatgrass hybrid at WL-5. Perhaps most noteworthy is that dry matter yield for Hycrest was equivalent to or significantly greater than

Table 3. Pearson correlation coefficients (r) for regressions of carbon isotope discrimination (Δ) and total dry matter yield in 14 perennial, cool-season grasses at 3 water levels (WL) across 2 years (n = 14).

		Δ		Dry matter yield		
		WL-3	WL-5	WL-1	WL-3	WL-5
Δ	WL-1	0.67**	0.51	0.05	0.14	0.17
	WL-3		0.88**	0.45	0.54*	0.44
	WL-5			0.45	0.60*	0.41
Dry matter yield	WL-1				0.92**	0.46
	WL-3					0.50
	WL-5					

*,** Significant at 0.05 and 0.01 levels of probability, respectively

Table 4. Mean squares from ANOVA for total dry matter yield of 14 perennial, cool-season grasses at 3 water levels (WL) and combined across water levels, for each year separately and combined across 2 years.

		Dry matter yield			
Source	df	WL-1	WL-3	WL-5	Combined
		----(Mg ha^{-1})----			
1994					
Grass	13	10.45**	13.13**	3.73**	19.50**
Water level (WL)	5	——	——	——	127.46**
Grass x WL	65	——	——	——	3.89**
1995					
Grass	13	47.28**	29.88**	12.06**	66.27**
Water level (WL)	5	——	——	——	372.35**
Grass x WL	65	——	——	——	2.58**
Combined					
Grass	13	49.33**	37.24**	13.50**	72.79**
Water level (WL)	5	——	——	——	486.11**
Grass x WL	65	——	——	——	13.24**
Year	1	411.45**	299.68**	99.06**	762.26**
Grass x Year	13	8.39**	5.77**	2.59*	11.88**
WL x Year	5	——	——	——	24.42**
Grass x WL x Year	65	——	——	——	2.78**

*,**Significant at 0.05 and 0.01 probability levels, respectively

all other grassses at WL-5; however, Hycrest was in the higher tier of grasses for Δ at WL-5.

Discussion

Previous studies reported significant genetic variation for Δ in crested wheatgrass breeding populations, and the magnitude of the heritability estimates for Δ indicated that selection would be effective (Johnson et al. 1990, Read et al. 1993, Asay et al. 1998). Significant differences for Δ also were reported in orchardgrass, tall fescue, and perennial ryegrass, and the relative differences among species were consistent across irrigated and dryland conditions (Johnson and Bassett 1991). Asay et al. (1996) found significant differences for Δ among accessions and cultivars of Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski). They also reported that tetraploid accessions made more efficient use of water than diploid cultivars. Frank et al. (1997) examined Δ in diploid and tetraploid crested wheatgrass and western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) and reported that Δ was under genetic control and could likely be altered through breeding. In our study, significant differences also were observed for Δ among the 14 cool-season grasses we evaluated, particularly under the lowest water application. The range of mean Δ values found in our study (17–20.7‰) fell within the range of Δ values (16.1–23.1‰) reported by Smedley et al. (1991) in their survey of a wide range of 42 species within a perennial grassland community near Salt Lake City, Utah.

Hycrest crested wheatgrass and Magnar Basin wildrye exhibited different Δ responses in our study. Hycrest grows well in areas that receive less than 250 mm of annual precipitation (Asay et al. 1985) and typically becomes dormant during the hot, summer period. Although Magnar Basin wildrye also grows in areas that receive low amounts of precipitation, it usually prefers ravines, swales, and areas with high water holding capacity that are favorable micro-environments. In our study, Hycrest consistently exhibited the highest Δ value (presumed lowest water-use efficiency) across water levels, whereas Magnar showed 1 of the lowest Δ values (presumed highest water-use efficiency). Initially, these responses seemed opposite from those expected. However, the higher values of Δ for Hycrest probably reflect its rapid, early vegetative growth in the spring compared to Magnar, which initiates growth later in the spring and produces much of its growth later in the summer than Hycrest. As a result, Hycrest probably has a high Δ because it produces most of its vegetative growth in the early spring when water is most available and stomatal limitations to water stress are minimal. In contrast, the low Δ values for Magnar probably reflect the prolonged activity of Magnar during more stressful conditions of the summer with greater stomatal limitation and subsequently lower Δ values than Hycrest. Smedley et al. (1991) reported similar trends where they found a seasonal decrease in Δ values that reflected prolonged plant activity during the stressful conditions of summer compared to early spring.

Another interesting response comparison in our study was between Hycrest and hexaploid crested wheatgrass. The slopes for dry matter yield were 0.34 for Hycrest and 0.35 for the hexaploid; however, the intercept values were markedly different. For example, Hycrest exhibited about a 2.5 Mg ha^{-1} greater dry matter yield than the hexaploid at WL-1; however, values of Δ were nearly the same for Hycrest and the hexaploid at WL-1. The similar Δ values at WL-1 suggest similar transpiration and gas exchange patterns for Hycrest and the hexaploid, but the dry matter yields are very different. Hexaploid crested wheatgrass has numerous, wide leaves compared to Hycrest so the hexaploid has a high leaf to stem ratio compared to Hycrest. Thus, part of the explanation in differential responses between these 2 crested wheatgrasses could be related to this difference in plant type, which was discussed by Brugnoli and Farquhar (2000).

Other factors that can influence responses in Δ include factors such as growth conditions, resistance between the intercellular spaces and sites of carboxylation, the effects of carbon losses during respiration and photorespiration, mineral nutrition of plants, and translocation of carbon among various plant parts (Farquhar et al. 1989). When the influence of these other components is substantial, the observed results for carbon isotope discrimination (Δ) can show a deviation from the expected response (Brugnoli and Farquhar 2000). As a result, although individual grasses may appear to differ in water-use efficiency based on differences in Δ, these differences may reflect differences in other plant characteristics. For example, although Hycrest crested wheatgrass initiates growth early in the season and may produce considerable dry matter during this low stress period, Hycrest also may be able to extract soil water more effectively than the other grasses and, thereby, maintain a better water balance and produce greater dry matter yield at drier levels than the other grasses.

Dry matter yield is conditioned by many other genetic factors in addition to those associated with Δ. In C_3 crop species, relationships between Δ and dry matter yield are sometimes positive and other times negative depending on the particular environmental conditions of the study (Brugnoli and Farquhar 2000). In early studies with clonal lines of crested wheatgrass, we found that Δ was positively correlated with dry matter yield, suggesting that selection for higher water-use efficiency would be accompanied by lower dry matter yield (Johnson et al. 1990). However, in later studies we found that dry matter yield was not correlated with Δ in crested wheatgrass breeding lines, indicating that genetic alteration of these 2 traits could be achieved concurrently (Read et al. 1992, 1993, Asay et al. 1998). Positive associations between Δ and dry matter yield probably would not be a major concern because dry matter yield is usually 1 of the primary selection criteria for evaluating breeding lines in most forage improvement programs. As a result, even though Δ may be positively related to dry matter yield in some situations, dry matter yield would be routinely evaluated and used as a primary selection factor in the breeding effort. Thus, Δ would most likely be used in a forage breeding program as 1 of several secondary selection criteria incorporated into a selection index.

In summary, we found that Δ decreased in a near linear manner from the wettest to driest water levels and that Δ varied significantly among the 14 perennial cool-season grasses that we evaluated, particularly at the lowest water level. We also found that dry matter yield decreased across water levels and differed significantly among the 14 grasses at the various water levels; however, the rate and manner of decline varied among grasses. In general, Δ was not closely associated with dry matter yield, suggesting that breeding efforts to improve these species should involve simultaneous selection for both dry matter yield and Δ. Additional research is needed to clarify the complex interactions among Δ, gas exchange, water relations, dry matter yield, and their interaction with environmental factors in these cool-season, perennial grasses.

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J. Range Manage.
56: 660-664 November 2003

Germination of seeds of Fremont cottonwood

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Abstract

Fremont cottonwood (*Populus fremontii* S. Watson) is the most important cottonwood species of the southwestern United States. It is usually found in riparian areas of desert riverine systems. Often it is the only tree species in such environments. Lack of Fremont cottonwood seedling recruitment is of concern in many areas. This is especially an issue in river systems infested with the exotic saltceder (*Tamarix ramosissima* Ledeb.). The proposed suppression of saltceder with a biological control agent, raises the question of the spontaneous recruitment of Fremont cottonwood seedlings if competition is reduced from exotic woody species. Several studies have stressed that geomorphologic-hydrologic conditions in riparian habitats control safesites for Fremont and other cottonwood species seed germination and seedling establishment. Our purpose was to investigate the physiological amplitude for Fremont cottonwood seeds to germinate under a wide range of constant or alternating temperatures. Immediately after dispersal the seeds of Fremont cottonwood are highly germinable. In each of the 3 years that seeds were collected multiple temperature regimes supported 100% germination. Optimum germination averaged over 90%. At moderate to high warm period temperatures, most germination that will occur does so during the first week after imbibition of moisture. Temperature regimes that supported optimum germination at least once ranged from 0/5° C to 25/40° C. The regimes that always supported optimum germination were in 2 distinct group: 2/25 and 2/30° C; and a wider dispersed group with 15, 25, or 25° C cold period temperatures and 25, 30, or 35° C warm period temperatures. There was one outlier at 10/15° C. Fremont cottonwood seeds are highly and rapidly germinable at a wide range of temperatures.

Key Words: ***Populus fremontii*, temperature profiles, *Tamarix ramosissima*, seedbed temperatures**

Resumen

"Fremont cottonwood" (*Populus fremontii* S. Watson) es la especie de "Cottonwood"más importante del suroeste de Estados Unidos, usualmente encontrada en las áreas ribereñas de los sistemas de ríos de los desiertos y a menudo es la única especie de arbórea en estos ambientes. La falta de establecimiento de plántulas de "Fremont cottonwood" es una preocupación en muchas áreas. Esto es especialmente un problema en los sistemas de ríos infestados por la especie invasora "Saltceder" (*Tamarix ramosissima* Ledeb.). La propuesta de suprimir el "Saltceder" mediante un agente de control biológico produce la pregunta respecto al establecimiento espontáneo de plántulas de "Fremont cottonwood" si la competencia con las especies exóticas leñosas se reduce. Varios estudios has enfatizado que las condiciones geomorfológicas-hidrológicas de los hábitats ribereños controlan los sitios seguros para el "Fremont" y la germinación de la semilla y establecimiento de plántulas de otras especies de "Cottonwood". Nuestro propósito fue investigar la amplitud fisiológica de las semillas de "Fremont cottonwood" para germinar bajo un amplio rango de temperaturas constantes y alternantes. Inmediatamente después de la dispersión las semillas de "Fremont cottonwood" son altamente germinables. En cada uno de los 3 años que las semillas fueron colectadas múltiples regímenes de temperatura produjeron 100% de germinación, la germinación óptima promedio más del 90%. En periodos de temperatura de moderada a alta la mayoría de la germinación ocurrirá durante la primer semana después de la imbibición de humedad. Los regímenes de temperatura que sostuvieron al menos una vez la germinación óptima variaron de 0/5° C a 25/40° C. Los regímenes que siempre mantuvieron la germinación óptima estuvieron en 2 grupos distintos 2/25 y 2/30° C; y un grupo de mayor dispersión con 15, 25, or 25° C de temperatura en el período frío y 25, 30, or 35° C en el período de temperaturas calientes. Hubo un régimen de temperatura fuera del patrón 10/15° C. Las semillas de "Fremont cottonwood"son alta y rápidamente germinables en un amplio rango de temperaturas.

Fremont cottonwood (*Populus fremontii* S. Watson) is the cottonwood of the southwestern United states (Sudworth 1908). It is closely associated with desert riparian habitats. It is often the tree of riparian areas where streams and rivers extending out from mountainous watersheds into desert valley. Often Fremont cottonwoods form gallery forest over desert streams creating an arboreal environment in sharp contrast to the stark desert or regimented irrigated field that surround the woodland. Historically, the gallery forest often transect the primary sites for irrigated agriculture, ranching, and urbanization (Aspund and Gooch 1988).

Fremont cottonwood reproduction usually is restricted to what has been described as a strand line environment (Siegel and Brock 1990). The natural habitat for Fremont cottonwood seedling recruitment is a portion of the complex geomorphology formed by meandering streams subject to seasonal flooding (Aspund and Gooch 1998). The seeds of Fremont cottonwood are wind dispersed to damp gravel, sand, or silt bars where germination occurs and the roots of the seedlings follow the seasonal declining water table. In many areas Fremont cottonwood seedling recruitment has been virtually non-existent. This has been variously attributed to flooding that results in scouring of the riparian area, channelization to reduce damage from flooding, construction of upstream damns to prevent flooding, phreatophytic plant control, invasion by phreatophytic plants especially tamarisk (*Tamarix ramosissima* Ledeb.), agricultural practices, and over grazing. Most of the studies concerning the lack of

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Manuscript accepted 10 Dec. 02.

seedling recruitment have focused on the hydrology of Fremont cottonwood habitats with little attention to the physiology and ecology of the seeds themselves.

The lack of detailed seed physiology research on seeds of Fremont cottonwood is partially a function of the short viability period of the seeds. In laboratory storage, seeds of Fremont cottonwood lost all viability after 7 weeks (Horton et al. 1960). In commercial forest tree nurseries, cottonwood seeds were reported to have markedly reduced emergence if planting was delayed 2 days after harvest (Engstrom 1948).

A major concern with the proposed use of biological control agents to suppress invasive populations of tamarisk is the probability of subsequent recruitment of seedlings of native woody species to form habitat for dependent birds. In a previous paper we reported on the germination of seeds of native willow (*Salix* sp.) species growing in tamarisk infested areas of the delta of the Walker River in western Nevada (Young and Clements 2003). The only other native woody species in the delta is Fremont cottonwood.

Our purpose was to determine the germination of Fremont cottonwood seeds at a wide range of constant and alternating incubation temperatures. This is a first step in understanding the germination ecology of the seeds of this tree species.

Materials and Methods

Fremont cottonwood seeds were collected from splitting capsules as soon as seed dispersal was evident. Seed collections were made in 1999, 2000, and 2001. Seeds were collected from as many trees as possible bulked into 1 collection for each year. All collections were made in the delta of the Walker River between Schurz, Nevada and Walker Lake (Latitude north 38° 53.534', Longitude west 118°, 46.773'). The seeds were immediately transported to the laboratory and counted into Petri dishes without removing the abundant silky hairs that cover the seed.

In all experiments 4 replications of 25 seeds each were used in a randomized block design. Seeds were placed on top of non-toxic commercial germination paper in closed Petri dishes and kept wet with tap water. Germination trials were conducted in the dark. Incidental light was received during initial wetting and germination counts. Seeds were considered germinated when the radical emerged 1 mm. Germination counts were made after 1, 2, and 4 weeks. Constant incubation temperatures were 0, 2, and 5° C and at 5 degree increments through 40° C. Alternating regimes included 16 hours at each constant temperature, plus 8 hours at each possible higher temperature per 24 hours. For example, 35 C alternated with 40° C only, while 0° C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40° C. This made a total of 55 constant and alternating temperature regimes (Young et al. 1991).

The germination responses of the accessions of Fremont cottonwood were compared using the following seedbed temperature regime definitions (Young and Evans 1982):

a. Very cold: 0/0 (constant 0° C), 0/2 (0° C for 16 hours and 2° C for 8 hours in each 24 hour), 0/5 and 2/2° C.
b. Cold: 0/10, 0/15, 2/5, 2/10, 2/15, 5/5, and 5/10° C.
c. Cold fluctuating: 0/20 through 0/40° C and 2/20 through 2/40° C.
d. Fluctuating: 5/35 through 5/40° C, 10/35, 10/40, an 15/40° C.
e. Moderate: 5/20 through 5/30, 10/10 through 10/30° C, 15/15 through 15/35° C, 20/20 through 30/35° C, and 25/25 through 25/30° C.
f. Warm: 20/40, 25/35, and 25/40° C, 30/30 through 30/40° C, 35/35, 35/40, and 40/40° C.

The temperature categories reflect germination environments of field seedbeds based on several years of monitoring in the Great Basin (Evans et al. 1970, Evans and Young 1970, 1972).

Data from each base temperature and its alternating temperature regimes were used to generate a quadratic response surface with estimated means and confidence intervals at the 1% level of probability (Young et al. 1980, Evans et al. 1982, Palmquist et al. 1987). A number of germination parameters were calculated from the quadratic response surfaces (Table 1) (Young and Evans 1982). These germination parameters were individually subjected to analysis of variance and the means separated by Duncan's Multiple Range Test.

Results and Discussion

The freshly dispersed seeds of Fremont cottonwood germinate over a wide range

Table 1. Germination parameters calculated from quadratic response surfaces (Young and Evans 1982).

Calculated parameters	Derivation of parameter	Purpose
Calculated within profile:		
Mean germination	Sum divided by 55	Gross comparison of profiles
Percentage of regimes with germination	Number with germination divided by 55	Indication of breath of germination response
Percentage of regimes with optima	Number of regimes with germination not less than the maximum observed minus one half the confidence interval divided by 55	Provides indication of the breath of temperatures that support optimum germination
Mean of optima	Sum of optima divided by number of regimes with optima	Provides a measure of potential germination at most desirable temperatures
Maximum germination	Highest observed germination	Indication of potential viability
Calculated among germination profiles		
Frequency of optima	Times a given temperature supports optimum germination divided by the total number of test	Provides an estimate of optimum temperatures for germination with precision

Table 2. Quadric response surface with calculated percentage germination and confidence interval ($P \leq 0.01$) for seeds of Fremont cottonwood incubated at 55 constant or alternating temperatures. Seeds collected from Walker River Delta in 2000.[1]

Cold period temperature	Percentage germination Warm period temperature C 0	2	5	10	15	20	25	30	35	40
	(%)									
0	30±8	75±8	[100±8*	100±8*	100±8*	100±8*	100±8*	100±8*	100±8*	100±8*]
2		73±10	97±8*	[100±8*	100±8*	100±8*	100±8*	100±8*	100±8*]	96±10*
5			95±9*	[100±8*	100±8*	100±8*	100±8*	100±8*	100±8*	100±8*]
10				[100±8*	100±8*	100±8*	100±8*	100±8*]	95±10*	88±10
15					[100±8*	100±8*	100±8*	100±8*	100±8*]	30±10
20						[100±8*	100±8*	100±8*]	90±10	30±12
25							77±10	96±10*	45±10	12±12
30								16±10	4±12	6±12
35									0±12	0±12
										0±12

[1] Number following the mean is one half of the confidence interval as determined from regression equations used to develop response surface (Palmquist et al. 1987). The maximum calculated germination is enclosed by brackets{[ ]. * indicates mean not lower than the maximum germination minus one half of its confidence interval, our definition of optimum germination.

of constant or alternating temperatures (Table 2). We present the complete response surface for the germination of seeds collected in 2000 to illustrate the basic data set. A staggering 53% of the temperature regimes produced 100% germination. This is a level of viability unprecedented in our experience with seeds collected from native stands. The number of regimes with 100% germination was much higher in 2000 compared to 1999 and 2001 (data not shown). In early May of 2000, just a few weeks before the Fremont cottonwood seeds were mature, a severe late frost occurred. Germination of seeds of 2 species of willow (*Salix*) collected in the same area as the Fremont cottonwood seeds was severely reduced (Young and Clements 2003).

Mean germination of the profiles and number of regimes supporting germination for the 3 years of testing did not significantly ($P \geq 0.01$) differ (Table 3). Regimes with some germination is an important parameter because even a limited germination potential under harsh seedbed temperature conditions maybe mean the difference between some seedling recruitment and complete failure. If you could successfully recruit 1 Fremont cottonwood seedling per linear kilometer of riparian habitat on an annual basis stand renewal rates might be considered sustainable. This is just a hypothetical estimate which is not based on any data, but it illustrates the importance of germination at a very wide range of incubation temperatures and the increased chance of establish if the seeds of a moderately long lived perennial woody species can germinate at some level at temperature extremes. For Fremont cottonwood seeds produced in 2000 in the Walker River delta, there was 30% germination at a constant 0° C and 100% germination at 0/40° C (0° C for 16 hours and 40° C for 8 hours in each 24 hour period) (Table 2).

Table 3. Germination parameters for seeds of Fremont cottonwood calculated from quadratic response surfaces. Seeds of all accessions from Walker River Delta.[1]

Germination Parameter	Accession 1999	2000	2001
	(%)		
Profile characteristics			
Mean	75	76	72
Regimes with some germination	92	94	96
Mean of optima	92	99	99
Regimes with optima	42b	69a	58ab
Maximum	100	100	100
Seedbed temperature categories			
Very cold	28b	70a	10b
Cold	87	99	91
Cold fluctuating	86	99	83
Fluctuating	86	99	83
Warmer	77a	15b	65b
Moderate	87	93	97

[1] Means within rows followed by the same letter are not significantly different at the 0.01 level of probability as determined ny Duncan's Multiple Range Test. No letter indicates no significant differences.

For seeds produced in 2000 and 2001, over 50% of the temperature regimes supported optimum germination (Table 3). Our definition of optimum germination is not lower than the maximum observed minus one half of the confidence interval ($P \geq 0.01$). In all years the optima averaged over 90%. In all 3 years the maximum observed germination was 100%.

The categories of seedbed temperatures which we use were developed for terrestrial seedbeds during the late fall or early spring germination period (Evans et al. 1970). Fremont cottonwood seed germination has to occur soon after dispersal in late May and early June. It is doubtful that very cold seedbed temperatures would occur during the germination (0, 2, 0/2, and 0/5° C). Freezing night time temperatures are possible, but not probable. The Fremont cottonwood seeds collected in 2000 averaged 70% germination at these temperatures and had 30% germination at 0° C (Table 2). The seeds collected in all 3 years had very high germination at the cold category of seedbed temperatures (Table 3). The seeds collected in 2000 that had very high germination at very cold and cold temperatures had significantly ($P \geq 0.01$) lower germination at warmer seedbed temperatures (Table 3).

Fremont cottonwood seeds combine the requirement to fall on a moist seedbed with a very short viability half life. This makes speed of germination an important parameter. During the first week of incubation with 0 to 5° C cold period temperatures the warm period temperatures had to be 15° C or above to produce 50% of the total germination observed with 4 weeks

Table 4. Percentage of total germination of Fremont cottonwood seeds that occurred during the first week of incubation at each of the 55 temperatures tested. Average for all seeds collected from Walker River Delta 1999, 2000, and 2001.

Cold period temperatures					Percentage of total germination Warm period temperatures C					
	0	2	5	10	15	20	25	30	35	40
(C)					-(%)-					
0	0	27	19	17	50	65	90	94	98	68
2		6	30	29	64	75	94	97	98	64
5			6	35	62	75	90	97	97	91
10				58	81	92	90	90	99	100
15					2	98	95	98	100	100
20						95	98	99	100	97
25						95	98	99	100	97
30							89	99	100	100
35									98	100
40										0

Table 5 Percentage of total germination of Fremont cottonwood seeds that occurred during the second week of incubation at each of the 55 temperatures tested. Average for all seeds collected from Walker River Delta 1999, 2000, and 2001.

Cold period temperatures					Percentage of total germination Warm period temperatures C					
	0	2	5	10	15	20	25	30	35	40
(C)					-(%)-					
0	0	30	40	50	50	35	7	5	0	32
2		48	46	52	32	20	6	3	2	36
5			69	64	23	25	10	3	3	5
10				40	11	8	9	3	0	0
15						8	2	5	1	0
20						5	2	1	0	3
25							9	0	0	0
30								2	1	2
35									0	0
40										0

of incubation (Table 4). A constant 10° C would also produce above 50% of the observed germination. To get above 90% of the observed germination in the first week the cold period temperature had to be 10 through 20° C alternating with at least 20° C or any cold period temperature alternating with 25° C. To reach 100% of the observed germination in the first week cold period temperatures had to be 10° C or above and the warm period temperatures in the 35 or 40° C categories. In interpreting these results it is important to remember the data is presented as the percentage of the total observed that occur in the first week of incubation. For example a 25/40° C temperature regime had 100% of the observed germination in the first week (Table 4), for the seed collected in 2000 the total germination was only 12%. A 0/10° C incubation temperature had only 17% of the total observed germination in the first week (Table 4), the total germination for 2000 seed after 4 weeks was 100% (Table 2). At high temperatures during the warm period, the germination you are going to observe happens very quickly, but it is not necessarily high germination.

During the second week of incubation

Table 6. Percentage of total germination of Fremont cottonwood seeds that occurred during the third and fourth weeks of incubation at each of the 55 temperatures tested. Average for all seeds collected from Walker River Delta 1999, 2000, and 2001.

Cold period temperatures					Percentage of total germination Warm period temperatures C					
	0	2	5	10	15	20	25	30	35	40
(C)					-(%)-					
0	100	45	41	33	0	0	3	0	2	0
2		44	29	19	4	5	0	0	0	2
5			25	1	15	0	0	0	0	0
10				2	8	0	1	7	1	0
15					0	0	0	1	0	0
20						0	0	0	0	0
25							2	1	0	0
30								0	0	1
35									0	0
40										0

Table 7. Frequency that a given temperature regime supported optimum germination of seeds of Fremont cottonwood for all accessions tested.

Cold period temperatures	Frequency Warm period temperatures C									
	0	2	5	10	15	20	25	30	35	40
(C)	-(%)-									
0			25	25	75	50	50	50	50	25
2				50	75	75	100	100	50	25
5			25	50	75	75	75	75	50	25
10				75	100	75	75	75	50	
15					50	75	100	75	100	25
20						75	75	100	50	25
25							50	100	75	50
40									25	

germination at the higher incubation temperatures was minimal and sporadic (Table 5). An exception was 0/40 and 2/40° C where about two thirds of the total observed germination occurred during the first week and one third during the second week of incubation (Table 4 and 5). The low cold period temperatures alternating with cool warm period temperatures had moderate amounts of their total observed germination during the second week of incubation (Table 5). Only a constant 0°C had all the observed germination during the third and fourth weeks of incubation (Table 6). Smaller amounts of germination occurred for the cooler incubation temperatures. These results indicate that with moderate to high warm period temperatures, most of the germination of Fremont cottonwood seeds that will occur does so during the first week after they imbibe moisture, even if cold period temperatures are quite cold.

With so many temperatures supporting optimum germination it is expected that the frequency of optima would be spread over a wide range (Table 7). Temperature regimes from a cold 2/5° C to a warm 25/40° C supported optimum germination at least once. The regimes that always supported optima were found in 2 distinct groupings. The first was 2/25 and 2/30° C (Table 7). The second group was 20/25 and 20/35° C, 20/30° C, and 30° C. There was one outlier at 10/15C. With the exception of the outlier, the warm period temperature had to be 25 or 30°C.

Viability, dormancy, and speed of germination do not appear to be limiting for germination of Fremont cottonwood seeds from the Walker River delta populations. This information reinforces the need to understand the moisture relations of available seedbeds during the seed dispersal period to understand the limiting factors for Fremont cottonwood seed germination.

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J. Range Manage.
56: 665-672 November 2003

Soil carbon, nitrogen and phosphorus in modified rangeland communities

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Abstract

Rangelands contain between 10 and 30% of global soil organic C reserves and may be an important sink for atmospheric CO_2, but less C tends to be stored in rangelands cultivated for agricultural use than undisturbed rangelands. Establishing perennial plant communities on formerly cultivated rangelands is expected to stabilize soil properties and increase the amount of C stored in rangeland soils, but there is little information on what plant communities are most effective at building soil C reserves. The purpose of this study was to compare soil C, N, and P pools in ungrazed native rangelands with ungrazed, unfertilized rangelands that were cultivated and then 1) abandoned, 2) seeded with non-native perennial grasses or legumes, or 3) cropped annually for 5 to 6 years. Three study sites in southern Alberta, Canada with native *Stipa-Bouteloua*, *Stipa-Bouteloua-Agropyron* and *Festuca campestris* plant communities represented the major ecotypes of the Northern Great Plains. The total C, N, and P content of rangeland soils were greatest at the *Festuca campestris* site, followed by the *Stipa-Bouteloua-Agropyron* and *Stipa-Bouteloua* sites, probably due to climatic conditions (precipitation and temperature). Generally, soils under modified plant communities contained less total C and N than soils under native rangeland, but the total P content was related more to site preparation than experimental treatments. Soils under alfalfa, orchardgrass and bromegrass tended to have more total C and N than soils cultivated annually in continuous wheat or wheat-fallow systems. The accumulation of C and N in soils under permanent cover was not related to net primary productivity and may be influenced more by the chemical composition and rate of decomposition of plant residues.

Key Words: cultivated, introduced grasses, alfalfa, native rangeland, total nutrients, extractable nutrients

Resumen

Los pastizales contienen entre 10 y 30% de las reservas globales de C orgánico del suelo y pueden ser un importante depósito para el CO_2 atmosférico, pero menos carbón tiende a ser almacenado en los pastizales cultivados para fines agrícolas que en los pastizales sin disturbio. Se espera que el establecimiento de comunidades vegetales perennes en las tierras cultivadas que primeramente fueron pastizales estabilice las propiedades del suelo e incremente la cantidad de C almacenado en los suelos de pastizal, pero hay poca información sobre cuales comunidades de plantas son mas efectivas en crear las reservas de C del suelo. El objetivo de este estudio fue comparar las reservas de C, N y P en pastizales nativos sin apacentamiento contra pastizales sin apacentamiento ni fertilización que fueron cultivados y luego: 1) abandonados, 2) sembrados con especies de zacates perennes o leguminosas no nativos y 3) cultivados anualmente por 5 o 6 años. El estudio se desarrollo en tres sitios en el sur de Alberta, Canada con comunidades de plantas nativas de *Stipa-Bouteloua*, *Stipa-Bouteloua-Agropyron* y *Festuca campestris* que representaron los principales ecotipos de las Grandes Planicies del Norte. El contenido total de C, N, y P de los suelos de pastizal fue mayor en el sitio de Festuca campestris, seguido por los sitios de *Stipa-Bouteloua-Agropyron* y *Stipa-Bouteloua*, probablemente debido a las condiciones climáticas (precipitación y temperatura). Generalmente los suelos bajo comunidades de plantas modificadas contuvieron menos C y N total que los suelos de pastizal nativo, pero el contenido total de P se relaciono mas a la preparación del sitio que a los tratamientos experimentales. Los suelos con alfalfa, "Orchardgrass" y "Bromegrass"tendieron a tener mas C y N total que los suelos cultivados anualmente con los sistemas trigo continuo o trigo-descanso. La acumulación de C y N en suelos con cubierta permanente no estuvo relacionada con la productividad primaria neta y puede estar influenciado mas por la composición química y la tasa de descomposición de los residuos de plantas.

Grazing lands contain an estimated 10 to 30% of the world's soil organic C and, depending on how they are managed, have the potential to act as a significant sink of atmospheric CO_2 (Schuman et al. 2002, Lal 2002). A considerable portion of the rangeland in the Great Plains of North America was cultivated for agricultural use in the last 100+ years, causing a 24 to 60% reduction in the soil organic C pool (Gebhart et al. 1994). Intense cultivation (i.e., moldboard plowing) disrupts soil aggregates and fragments organic matter, accelerating decomposition, increasing microbial activity and stimulating the emission of CO_2 from soils (Anderson and Coleman 1985, Burke et al. 1995). The C input from agricultural crops is generally lower than from rangeland plant communities because more of the above-ground biomass may be removed from the ecosystem and because annual crops produce less root biomass than perennial grasses (Burke et al. 1995). Management practices that stabilize soil properties and

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Authors wish to thank S. Foran, J. Carefoot, and M. Crowe assistance with soil sampling and laboratory analysis.
Manuscript accepted 20 Jan. 2003.

promote primary production in rangelands are expected to sequester more C and reduce CO_2 emissions.

There is growing interest in converting marginal and eroded cropland in the arid and semi-arid Great Plains into grasslands. If cropland is abandoned, it can take many years for native plant communities to reestablish. Dormaar et al. (1994) found that the vegetation in *Stipa-Bouteloua* community, cultivated for wheat production for 3 years and then abandoned and grazed, reverted to a community dominated by *Stipa comata*, with very little *Bouteloua gracilis*. In the United States, native perennial grasses have been seeded on highly eroded cropland in the Great Plain states under the Conservation Reserve Program (Dunn et al. 1993). In other regions of the Great Plains, cultivated land has been restored or improved by seeding monocultures or mixtures of non-native perennial grasses (Lawrence and Ratzlaff 1989).

The establishment of permanent cover on formerly cultivated lands can quickly stabilize some soil properties, increasing water retention and reducing the quantities of sediments, nutrients and agrochemicals transported to surface waters within a few years (Dunn et al. 1993). It appears to take much longer for soil chemical and biological properties to recover after cultivation ceases. Dormaar and Smoliak (1985) reported that it took more than 50 years for the soil organic C content of abandoned cropland to approach the level of native rangeland. Five years after establishment of permanent grass cover, Gebhart et al. (1994) observed a 21% increase in soil organic C content in the 5 to 10 cm soil depth, but there was significantly less organic C in formerly cultivated land than native grasslands. In the first 10 years after cropland was converted to grassland, Baer et al. (2000) found no change in the total C and N pools, but an increase in microbial biomass C and N pools. Total C and N, microbial biomass and mineralization potentials were lower in the recently established grasslands than native grassland (Baer et al. 2000). If we hope to increase C sequestration on formerly cultivated lands in the Great Plains, we must first understand how cultivation has altered soil chemical and biochemical properties and then determine what management practices will be most effective at building the soil organic C reserves.

We examined selected soil characteristics at 3 sites along a climatic gradient in the Northern Great Plains. Between 5 and 6 years earlier, native rangeland was cultivated and then 1) abandoned, 2) seeded with non-native perennial grasses or legumes to establish a permanent cover, or 3) converted to agricultural land for annual crop production. We hypothesized that the reserves of total C, N, and P would decline after cultivation, relative to native rangeland, but the decline would be lower in plots that were abandoned or planted with perennial plants than those plots that were cultivated repeatedly for annual crop production. We also hypothesized that the decline in total C, N, and P reserves after cultivation would be greater in the driest, hottest site where decomposition would be more rapid than at the site with more rainfall and cooler soil temperatures. Extractable N and P pools were expected to be greater in cultivated soils than soils under permanent cover because we hypothesized that the roots of perennial crops had a greater capacity to remove N and P from the soil solution than the roots of annual crops. The objective of this study was to compare selected soil properties of modified plant communities (monocultures of annual agronomic crops, perennial introduced grasses or a perennial introduced legume) with native plant communities in ungrazed, unfertilized rangeland soils along a climatic gradient in the Northern Great Plains.

Materials and Methods

Site Description

The study was conducted at 3 sites in southern Alberta, Canada that are representative of major ecotypes of the Northern Great Plains. The sites were at the Agriculture and Agri-Food Canada Substation at Onefour, the Animal Diseases Research Institute (ADRI) near Lethbridge, and the Agriculture and Agri-Food Canada Substation west of Stavely in the Porcupine Hills. Information on the location (latitude/longitude), soil type, native plant community, and annual precipitation of each site is provided in Table 1. We refer to the sites by their native plant communities in this paper.

Experimental Treatments

In April 1993 (*Stipa-Bouteloua-Agropyron* and *Festuca campestris*) and April 1994 (*Stipa-Bouteloua*), 6 experimental treatments representing common production practices were established and compared with the native plant community in a randomized complete block design with 4 replicates. The experimental treatments (Table 2) were established in 3 x 10 m plots after cultivating the plots with a moldboard plow and seeding with introduced grasses, alfalfa, or wheat. In the abandoned treatment, the native plant community was cultivated several times during the first summer and volunteer plants that emerged from live tillers were removed until the spring of the second year. The experimental treatments were enclosed with a 4-strand barbed-wire fence that excluded livestock. Native plant communities in the study area and site preparation have been described by Moss and Campbell (1947), Coupland (1961) and Dormaar and Willms (2000a). This study began in the spring of 1999, which was 6 years after the experimental treatments were established at the *Stipa-Bouteloua-Agropyron* and *Festuca campestris* sites and 5 years after the experiment began at the *Stipa-Bouteloua* site.

Soil Analysis

Soil samples were obtained from the Ah soil horizon (0 to 15-cm depth) of plots at the 3 sites in the spring and in the fall after

Table 1. Soil and vegetation characteristics, and mean annual precipitation at the study sites.

Site	Location	Soil Classification		Prairie Classification	Native Vegetation	Average Precipitation
		Canada	US			
Onefour	49° 07'N 110° 29'W	Orthic Brown Chernozem	Aridic Haploboroll	Mixed	*Stipa-Bouteloua*	310 mm
ADRI	49° 43'N 112° 57'W	Orthic Dark Brown Chernozem	Typic Haploboroll	Mixed	*Stipa-Bouteloua-Agropyron*	420 mm
Stavely	50° 12'N 113° 57'W	Orthic Black Chernozem	Udic Haploboroll	Fescue	*Festuca campestris*	550 mm

Table 2. Experimental treatments established at the study sites.

Experimental Treatment	Species/cultivar	
	Stipa-Bouteloua and *Stipa-Bouteloua-Agropyron* sites	*Festuca campestris* site
Introduced grass #1	Crested wheatgrass (*Agropyron cristatum* L. Gaertn.)	Smooth bromegrass (*Bromus inermis* Leyss.)
Introduced grass #2	Russian wildrye (*Elymus junceus* Fisch.)	Orchard grass (*Dactylis glomerata* L.)
Alfalfa	*Medicago sativa* L. "Beaver"	
Spring wheat (continuous)	*Triticum aestivum* L. "Katepwa"	
Spring wheat/fallow rotation	*Triticum aestivum* L. "Katepwa"	
Abandoned	Native vegetation regrown after cultivation	

wheat harvest. In 1999, we collected samples on 12 May and 28 September (*Stipa-Bouteloua-Agropyron*), 20 May and 29 September (*Stipa-Bouteloua*) and 26 May and 30 September (*Festuca campestris*) whereas in 2000, we collected samples on 28 April (*Stipa-Bouteloua-Agropyron*), 5 May (*Festuca campestris*), and 19 May (*Stipa-Bouteloua*). Ten subsamples were collected from randomly selected locations within each experimental plot with a soil probe (3.2 cm internal diameter), composited, sieved (< 2 mm mesh) and then stored in sealed polyethylene bags at 4° C until analysis. Surface soil bulk density was determined in the fall of 1999 after harvest from undisturbed soil cores (3 cm length x 5.5 cm internal diameter) taken at the 0 to 3 cm depth. Bulk density (g oven-dried soil cm^3) in each core was determined after drying at 105° C for 48 hours (Blake and Hartge 1986).

Inorganic N and extractable P were measured on field-moist soil samples within 3 weeks of arrival at the laboratory. Soil moisture content was determined gravimetrically (105° C for 48 hours) and all concentrations were expressed per gram of dry soil. Inorganic N (NH_4-N and NO_3-N) was determined in 2M KCl extracts (1:5 soil:extractant) using the method of Maynard and Kalra (1993) and measured colorimetrically using the phenate and cadmium reduction-diazotization methods with a Technicon II flow-injection autoanalyzer (Technicon Industrial Systems, Tarrytown, N.Y.). Extractable P was determined in Kelowna (0.015M NH_4F + 0.25M CH_3COOH) soil extracts (1:10 soil:extractant) based on Van Lierop (1988). Ortho-phosphate was measured colorimetrically by the ammonium molybdate-ascorbic acid method (Murphy and Riley 1962) using a Technicon IV flow-injection autoanalyzer (Technicon Industrial Systems, Tarrytown, N.Y.).

A portion of soil collected from each site in the fall of 1999 was oven-dried (105° C for 48 hours), finely ground, and analyzed for total C, N, and P. Total C and N was determined by combustion with a Carlo-Erba CN analyzer (Milano, Italy). Total P was determined on a 1-g soil sample that was digested with H_2SO_4 and H_2O_2 with catalysts ($LiSO_4$ and Se powder) at 360° C for 2.5 hours (Parkinson and Allen 1975). Following digestion, the samples were analyzed colorimetrically for ortho-phosphorus using the ammonium molybdate-ascorbic acid method (Murphy and Riley 1962) on a Technicon IV flow-injection autoanalyzer (Technicon Industrial Systems, Tarrytown, N.Y.).

Plant Yields

Plant yields were measured at peak standing crop (late August to early September) each year from 1998 to 2000. A 0.25 m^2 subplot was harvested from each experimental treatment at a different sampling location each year. Vegetation in the subplot was clipped to ground level using hand clippers and sorted into dead (previous years' production) and live plant biomass. Live plant biomass was oven-dried (60° C for 48 hours), and the aboveground net primary production (ANPP) was calculated on a g dry matter m^{-2} basis. The net primary productivity (NPP) was estimated as follows:

$$NPP = ANPP_m + (ANPP_m \times R/S \text{ ratio}) \quad (1)$$

where $ANPP_m$ is the mean aboveground net primary productivity and R/S ratio is the root to shoot ratio used to estimate root production during a growing season.

Statistical Analysis

Data were evaluated statistically by ANOVA in a general linear model using SAS software (Version 8.02 for Windows, SAS Institute Inc., Cary, N.C., USA). The effects of experimental treatments and sampling time within a site were evaluated with a two-way ANOVA and compared with a protected LSD test at the 95% confidence level.

Results and Discussion

Soil bulk density was lower in undisturbed native rangeland than modified plant communities (Table 3). The bulk density tended to decline in plots with the same experimental treatment across sites, with *Stipa-Bouteloua* > *Stipa-Bouteloua-Agropyron* > *Festuca campestris*. Bulk density declines with increasing soil organic matter content because the quantity of air-filled pore space increases. The relationships between bulk density (BD) and the total soil C (SC) content (g C kg^{-1}) were:

$BD = 1.385 - 0.0295\ SC$; $R^2 = 0.51$, n=30 *Stipa-Bouteloua* site (2)

$BD = 1.469 - 0.0216\ SC$; $R^2 = 0.65$, n=30 *Stipa-Bouteloua-Agropyron* site (3)

$BD = 1.537 - 0.0111\ SC$; $R^2 = 0.53$, n=27 *Festuca campestris* site (4)

Table 3. Soil bulk density (0 to 3 cm depth) under native rangeland and modified plant communities in southern Alberta, Canada. Values are means ± standard errors.

Treatment	*Stipa-Bouteloua*	*Stipa-Bouteloua-Agropyron*	*Festuca campestris*
	($g\ cm^{-3}$)		
Native	0.79 ± 0.02	0.51 ± 0.04	0.39 ± 0.08
Crested wheatgrass	0.92 ± 0.05	0.81 ± 0.02	—
Russian wildrye	0.89 ± 0.06	0.89 ± 0.02	—
Smooth bromegrass	—	—	0.62 ± 0.03
Orchardgrass	—	—	0.59 ± 0.04
Alfalfa	0.97 ± 0.05	0.85 ± 0.02	0.69 ± 0.04
Continuous wheat	1.01 ± 0.05	0.99 ± 0.04	0.77 ± 0.02
Wheat-fallow	1.08 ± 0.04	0.94 ± 0.03	0.76 ± 0.04
Abandoned	0.91 ± 0.06	0.83 ± 0.01	0.60 ± 0.03

These relationships are similar to those reported by Bauer and Black (1992) for cropped agroecosystems, grazed, and relict grasslands in North Dakota. The slopes of the regression lines between BD and soil organic C ranged from –0.0128 to –0.0212, depending on soil texture (Bauer and Black 1992).

Total C, N, and P in soils

The total C, N, and P content of rangeland soils decline upon cultivation and it may take many years for soil nutrient pools to return to pre-cultivation levels (Dormaar and Smoliak 1985). To determine whether net gains or losses of total C, N, and P have occurred in the soil profile on a kg ha^{-1} basis, it is necessary to collect soil samples to perhaps a 2-m depth and determine the nutrient content and bulk density of each soil layer sampled (Lal 2002). Since we did not collect this information, our discussion will focus on differences in the total and available nutrient contents (g kg^{-1} soil basis) in the 0 to 15 cm layer of soils under native rangeland and modified plant communities.

Total C and N were significantly lower in soils under modified plant communities than native rangeland at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites, with the lowest total C and N contents in the continuous wheat and wheat-fallow treatments (Table 4). Soils under alfalfa had higher total C and N than the abandoned, continuous wheat, and wheat-fallow treatments at the *Stipa-Bouteloua* site, and a higher total C and N than the wheat-fallow treatment at the *Stipa-Bouteloua-Agropyron* site) (Table 4). Alfalfa can fix N_2 from the atmosphere, and this external input of N could contribute to a higher soil N content under alfalfa than some other treatments at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites. The higher soil C content in the alfalfa treatment than some modified plant communities was unexpected because our estimates suggest a lower NPP for alfalfa than most other plant communities (Table 5). The stabilization of C in soils is a complex process that depends on the activity of decomposers, primarily soil microorganisms. In most modified plant communities, microbial growth and biomass production may have been limited by N availability since no N fertilizers were added, but this was probably not the case in the alfalfa treatment. Nitrogen fixation in the alfalfa treatment could cause an increase in the microbial biomass, leading to greater microbial activity and the production of C-containing compounds that become stabilized in soils (dead microbial cells, polysaccharides and other byproducts of microbial metabolism). Moore et al. (2000) found that microbial biomass C and N concentrations were greater in soil under alfalfa than soils under continuous corn or continuous soybean production. They attributed these differences to the type and quantity of organic compounds released into the soil. Alfalfa residues (above-ground litter and dead roots) appeared to degrade more quickly than corn or soybean residues in the cropping systems examined. We would need to measure soil microbial biomass C and N pools and residue decomposition rates to determine whether these factors could explain differences in the soil C content of modified plant communities at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites.

The decline in total C and N in the wheat-fallow rotation compared to alfalfa was expected because the fallow phase of the rotation contributes little C through primary production and is cultivated, disrupting soil aggregates and accelerating C and N mineralization (Elliott 1986, Paustian et al. 1997). Soils under continuous wheat had less total C and N than soils under alfalfa at the *Stipa-Bouteloua* site, and less total N than soils under alfalfa at the *Stipa-Bouteloua-Agropyron* site. Although the net primary production (NPP) of the continuous wheat was similar to the NPP of alfalfa at the *Stipa-Bouteloua* site (Table 5), the net C input (C added in plant residues minus CO_2-C lost) from continuous wheat was probably lower than alfalfa because 35 to 45% of the above-ground biomass is removed when grain is harvested (Paustian et al. 1997). At the *Stipa-Bouteloua-Agropyron* site, there was no difference in total C from soils under continuous wheat or alfalfa, but the NPP of wheat was more than double the NPP of alfalfa (Tables 4 and 5). It was difficult to get an accurate estimate of ANPP in the alfalfa and wheat treatments at the *Stipa-Bouteloua-Agropyron* site because deer and rodents consumed some of the above-ground biomass before plant yields were taken. Better estimates of the NPP could improve our understanding of soil C dynamics at the *Stipa-Bouteloua-Agropyron* site.

At the *Festuca campestris* site, soils under native rangeland and orchardgrass had generally higher total C and N than other monoculture grass or cultivated treatments (Table 4). The total C and N content of soils under orchardgrass were similar to native rangeland 6 years after the modified plant community was established, which suggests that orchardgrass can increase the soil C and N content much more rapidly than the other perennial communities investigated. There tended to be more NPP and total C in soils under orchardgrass than other modified plant communities, suggesting a higher net C input into soils from orchardgrass (Tables 4 and 5). Orchardgrass has a higher root-to-shoot ratio than the native *Festuca campestris* vegetation or other modified plant communities (Table 5), and we propose that root production and turnover was responsible for the increase in soil C content under orchardgrass. We are not aware of other studies that show a more rapid increase in soil C pools under orchard-

Table 4. Total C, N, and P in soils under native rangeland and modified plant communities in southern Alberta, Canada.

Treatment	*Stipa-Bouteloua*			*Stipa-Bouteloua-Agropyron*			*Festuca campestris*		
	(g C kg^{-1})	(g N kg^{-1})	(mg P kg^{-1})	(g C kg^{-1})	(g N kg^{-1})	(mg P kg^{-1})	(g C kg^{-1})	(g N kg^{-1})	(mg P kg^{-1})
Native	21.6	2.08	346	42.4	4.00	575	101.4	8.70	907
Crested wheatgrass	15.1	1.58	330	29.1	2.90	528	—	—	—
Russian wildrye	14.8	1.55	326	28.0	2.81	524	—	—	—
Smooth bromegrass	—	—	—	—	—	—	84.2	7.44	959
Orchardgrass	—	—	—	—	—	—	96.6	8.27	981
Alfalfa	15.8	1.70	333	29.7	3.03	521	83.8	7.35	889
Continuous wheat	13.1	1.45	328	26.4	2.72	519	71.1	6.18	872
Wheat-fallow	13.3	1.43	318	25.5	2.70	521	80.5	7.00	928
Abandoned	13.9	1.50	315	29.1	2.93	538	81.3	7.15	910
LSD ($P < 0.05$)	1.9	0.18	26	3.6	0.27	22	10.5	0.93	93

grass than other plant communities, and further work is needed to confirm our findings.

Soils of the continuous wheat treatment at the *Festuca campestris* site had less total C than the orchardgrass, bromegrass and alfalfa treatments, and less total N than the orchardgrass, bromegrass, alfalfa and abandoned treatments (Table 4). However, only soils under orchardgrass had more total C and N than soils under the wheat-fallow treatment (Table 4). These results suggest that more C and N export occurred in the continuous wheat treatment, where grain was harvested and removed from the plots each year, than the wheat-fallow treatment. Weed biomass produced during the fallow phase was incorporated into the soil before the wheat crop was planted, which would add C and recycle the N taken up by weeds. Although differences in the total C and N content of soils may be related to differences in the NPP of continuous wheat and wheat-fallow treatments, it was difficult to obtain good estimates of NPP for these treatments. Yields (mean ± standard error) in the continuous wheat treatment were 199 ± 33 g m^{-2} in 1998, 830 ± 77 g m^{-1} in 1999 and 108 ± 17 g m^{-1} in 2000, which led to considerable variability in the mean ANPP values in the continuous wheat and wheat-fallow treatments (Table 5). Our findings suggests a higher net C input into soils under wheat-fallow than continuous wheat at the *Festuca campestris* site, but better above-ground biomass measurements are needed to confirm this possibility.

The total P content of soils varied little among experimental treatments. The total P content of soil was significantly higher in native rangeland than monoculture grass or cultivated treatments at the *Stipa-Bouteloua-Agropyron* site, but there was no difference in the total P content of native rangeland and most modified plant communities at the *Stipa-Bouteloua* and *Festuca campestris* sites (Table 4). Only a small proportion of the total P in soils is used for primary production, and it is recycled when plant residues are not exported from the site. Above-ground wheat biomass contains about 0.5% total P (Heyne 1987), and if grain was 45% of the above-ground biomass, then 4 to 9 kg P ha^{-1} would be removed from the continuous wheat and wheat-fallow treatments at harvest. This estimate is consistent with Campbell et al. (1997), who estimated 5.5 to 11.6 kg P ha^{-1} year^{-1} was exported in grain and hay from crop rotations in Saskatchewan. The few differences that emerged among experimental treatments are probably related to P removed in roots and soil when the sites were initially cultivated and raked (Dormaar and Willms 2000b). This finding is consistent with results from Elliott (1986), which showed that aggregate fractions contained less C, N and P when soils were cultivated than when they were left under native sod, but C and N losses from cultivated soils were much greater than P losses.

Although the loss of total C and N in soils under the same experimental treatments, relative to native rangeland, was similar at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites, much less total C and N was lost from soils at the *Festuca campestris* site. For instance, soils under continuous wheat contained between 38 and 39% less total C than native rangeland at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites, but only 28% less total C than native rangeland at the *Festuca campestris* site. These findings support our hypothesis that proportionately more C and N would be lost from the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites than the *Festuca campestris* site due to climatic conditions (rainfall and temperature). Dormaar and Willms (1993) found that roots from blue grama and rough fescue grasses decomposed more rapidly at the *Stipa-Bouteloua* site than the *Festuca campestris* site. They proposed that greater fluctuations in soil temperature and moisture at the *Stipa-Bouteloua* site than the *Festuca campestris* site contributed to physical comminution of roots, exposing a larger surface area for microbial colonization and decomposition. Fluctuations in soil temperature and moisture, particularly those associated with wet-dry and freeze-thaw cycles, may also accelerate the breakdown and decomposition of surface litter and destabilize soil aggregates, increasing C and N mineralization (Paustian et al. 1997).

The similarity in total C and N of soils under orchardgrass and native rangeland at the *Festuca campestris* site supports our hypothesis that recovery of total C and N in soils under permanent cover would occur more quickly at this site because it receives more rainfall and has cooler soil temperatures than the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites. In ungrazed prairies, the restoration of total C and N in soils under introduced grasses to the levels found in native rangeland also depends on the net C and N inputs from plant litter (above- and below-ground biomass), which may not be directly related to NPP. Lutwick and Dormaar (1976) found that soil (0–15 cm depth) under blue grama contained 25 g C kg^{-1} whereas soil under rough fescue contained 111 g C kg^{-1},

Table 5. Mean annual aboveground net primary productivity (ANPP), the root to shoot (R:S) ratio, and the estimated net primary productivity (NPP) in native rangeland and modified plant communities in southern Alberta, Canada.

Treatment	*Stipa-Bouteloua*			*Stipa-Bouteloua-Agropyron*			*Festuca campestris*		
	ANPP[1]	R:S ratio[2]	NPP	ANPP	R:S ratio	NPP	ANPP	R:S ratio	NPP
	(g m^{-2})		(g m^{-2})	(g m^{-2})		(g m^{-2})	(g m^{-2})		(g m^{-2})
Native	108 ± 18	8.7	1048	218 ± 30	8.7	2115	354 ± 42	4.0	1456
Crested wheatgrass	206 ± 26	6.7	1586	197 ± 23	6.7	1517	-	-	-
Russian wildrye	170 ± 15	15.1	2737	97 ± 13	15.1	1563	-	-	-
Smooth bromegrass	-	-	-	-	-	-	280 ± 25	2.9	1092
Orchardgrass	-	-	-	-	-	-	196 ± 18	7.6	1686
Alfalfa	142 ± 37	0.5	213	77 ± 18	0.5	116	335 ± 55	0.5	503
Continuous wheat	195 ± 39	0.2	234	258 ± 57	0.2	310	379 ± 100	0.2	455
Wheat-fallow	186 ± 73	0.2	223	95 ± 45	0.2	114	419 ± 161	0.2	503
Abandoned	160 ± 38	3.1	656	259 ± 26	3.1	1062	291 ± 34	4.0	1455

[1] Values are the means (± standard error) of ANPP (g dry matter m^{-2}) from 1998-2000 except the wheat-fallow treatment (mean ± standard error of ANPP from 1998-1999)

[2] Root:shoot (R:S) ratios from the following sources: native/abandoned *Stipa-Bouteloua/Stipa-Bouteloua-Agropyron* rangeland (Dormaar and Smoliak 1985), native/abandoned *Festuca campestris* rangeland (J.F. Dormaar, personal communication), crested wheatgrass and Russian wildrye (Willms et al. 2001), smooth bromegrass and orchardgrass (W.D. Willms, personal communication), alfalfa (Mapfumo et al. 1998), and wheat (Heyne 1987).

despite similar root biomass production. The net C input to soils is affected by the rate of decomposition of plant residues, and for the roots of rangeland plants, has been shown to depend on the C:N ratio, lignin and carbohydrate content of the residue (Herman et al. 1977). Further work is needed to verify the quantity and chemical composition of plant shoots and roots that enters the soils from modified plant communities to determine what proportions of C and N in plant litter are stabilized or lost from soils.

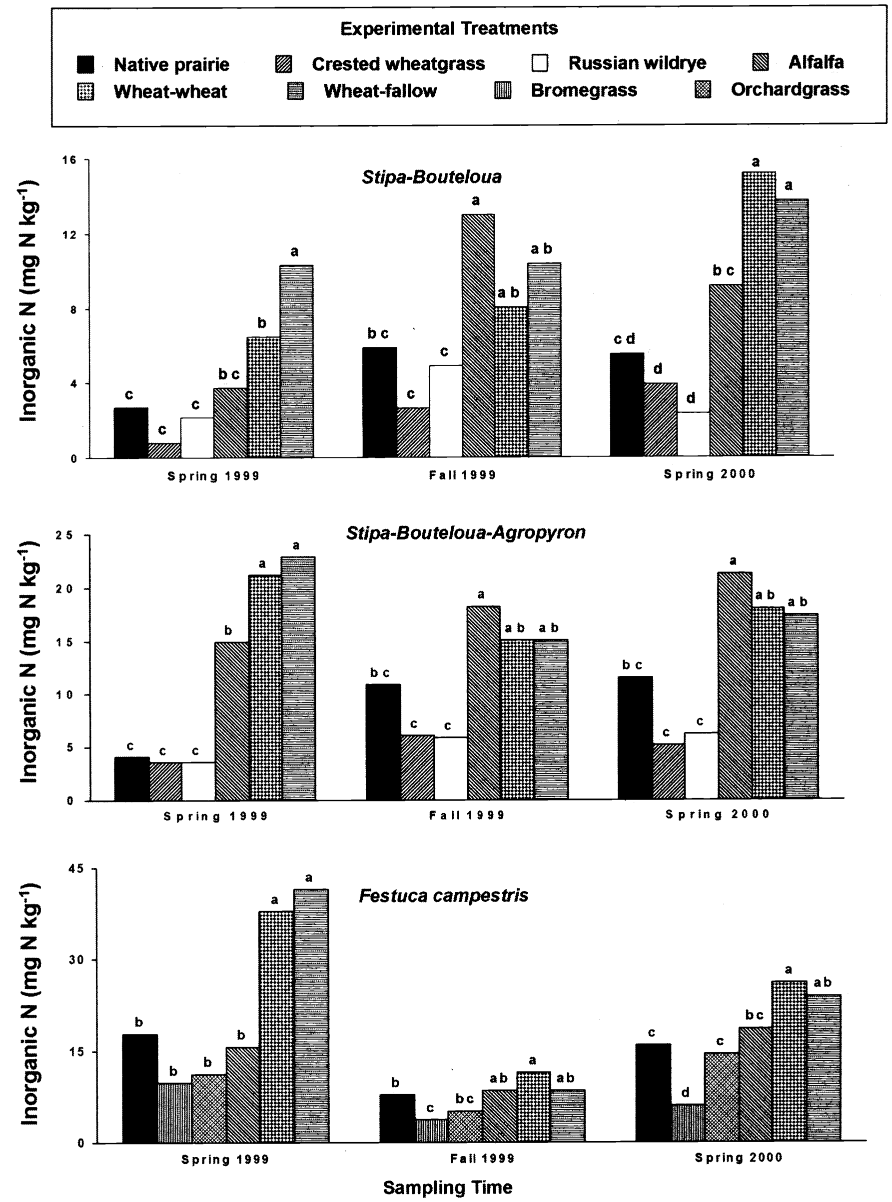

Fig. 1. Inorganic N (NH_4-N plus NO_3-N) concentrations in soils under native rangeland and modified plant communities at sites dominated by *Stipa-Bouteloua, Stipa-Bouteloua-Agropyron* and *Festuca campestris* vegetation. At each sampling date, mean values with the same letter are not significantly different at $P < 0.05$ (protected LSD test).

Extractable N and P in soils

We hypothesized that tillage would stimulate N and P mineralization, and therefore extractable N and P concentrations would be greater in cultivated soils than soils under perennial plant communities. At the 3 sites examined, the inorganic N pool was larger in soils of the 2 cultivated treatments (continuous wheat and wheat-fallow) than in soils under introduced grass monocultures at nearly all sampling dates (Fig. 1). There was more inorganic N in soils under alfalfa than introduced grass monocultures at most sampling dates in the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites, possibly because some of the N_2 fixed by the alfalfa was released into the soil solution during normal plant development or at senescence (Simpson 1976). Although soils under native rangeland tended to have lower inorganic N concentrations than cultivated soils, they had similar inorganic N concentrations as soils under the introduced grasses (Fig. 1). There are 2 possible explanations for this finding. One possibility is that introduced grasses and the plant communities of native rangelands absorb more inorganic N from soil solution than alfalfa or wheat. The fibrous root systems of introduced grasses and native plant communities could make them quite efficient at intercepting and absorbing NH_4-N and NO_3-N from the soil solution. The other possibility is that N immobilization by microbial biomass was higher in treatments with introduced grasses and native plant communities than alfalfa or wheat. Measurements of N uptake by different plant species and N immobilization by microorganisms under native and modified plant communities are needed to understand our results. Inorganic N that is not used by plants or soil organisms could be lost to the environment in leachates, surface runoff and gaseous products. We expect that N losses would be highest from the continuous wheat and wheat-fallow treatments, followed by the alfalfa treatment, and lowest from native rangeland and the introduced grass treatments. Further work would be needed to quantify N losses from native rangeland and modified plant communities.

Extractable P concentrations in soils at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites did not vary among treatments, although the extractable P levels tended to be greater in the fall than spring samples (Fig. 2). Higher extractable P levels suggest that more P is present in forms available for plant uptake in the fall than spring, which may be due to rapid uptake of plant-available P in the spring that depletes the extractable P reserves (Dormaar 1972). Plant-available P may originate from organic P compounds, and the potential activity of phosphatases responsible for P mineralization in the Mixed and Fescue Prairies peaks in February and declines in the early spring, possibly due to enzyme deactivation during spring thaw (Dormaar et al. 1984). Phosphatase activity measured by Dormaar and Willms (2000a) in the modified plant communities at the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites tended to

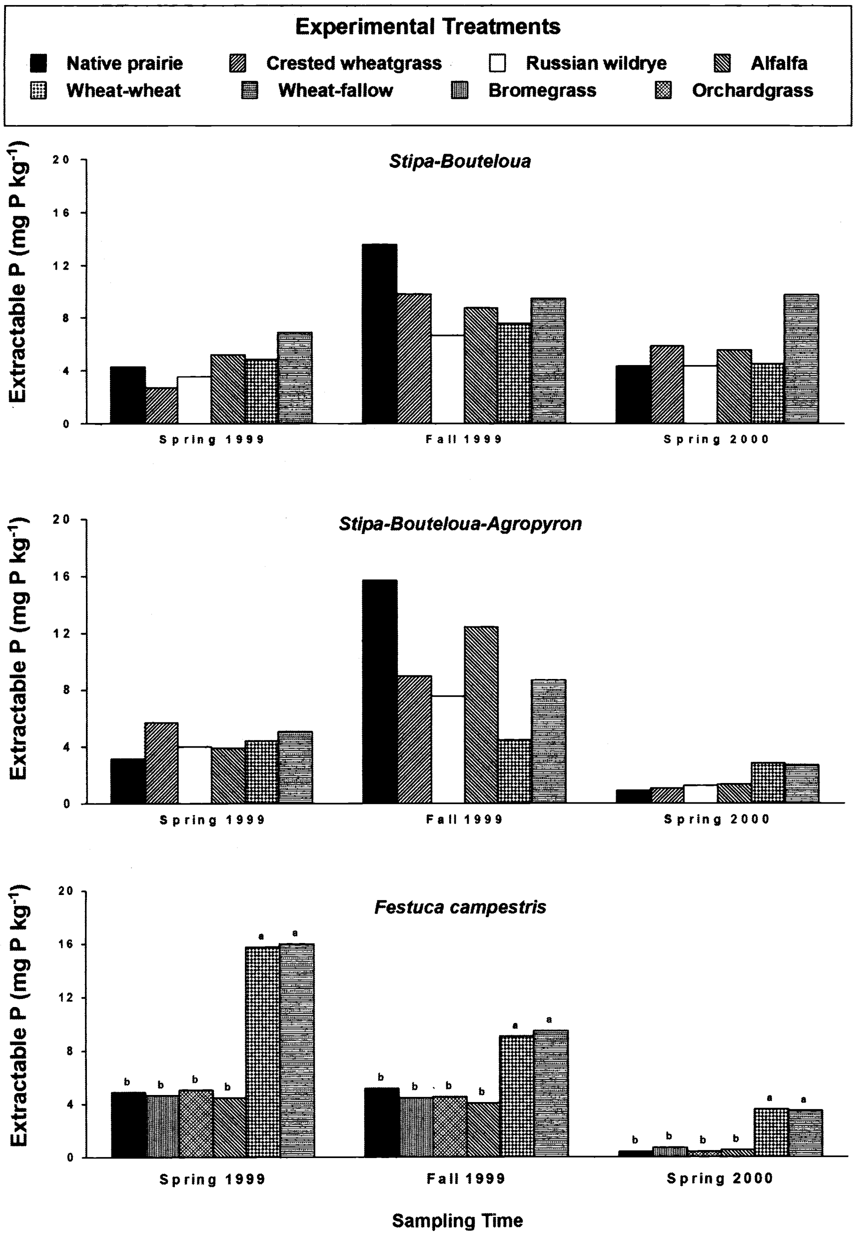

Fig. 2. Extractable P concentrations in soils under native rangeland and modified plant communities at a site dominated by *Stipa-Bouteloua*, *Stipa-Bouteloua-Agropyron* and *Festuca campestris* vegetation. At the *Stipa-Bouteloua* and *Stipa-Bouteloua-Agropyron* sites, there was no difference among treatments at each sampling date. At the *Festuca campestris* site, mean values with the same letter at each sampling date are not significantly different at P < 0.05 (protected LSD test).

be lower in the spring than the fall, which could explain the seasonal variation we observed in extractable P concentrations (Fig. 2). Plant-available P may also come from the dissolution of mineral-associated P complexes by organic acids (Bolan et al. 1994), and investigations are needed to determine whether the concentrations of organic acids capable of solubilizing mineral-associated P vary seasonally.

At the *Festuca campestris* site, there was more extractable P in cultivated soils than soils under perennial plant communities (Fig. 2). One possible explanation for this finding is that tillage stimulates decomposition, and organic acids produced during decomposition may have increased extractable P levels in the cultivated soils relative to other soils. Organic acids released during the decomposition of green manure, animal manure and organic residues increase P solubility by competing for P sorption sites, dissolving precipitated P compounds, altering surface charge, or forming organo-mineral complexes with Al, Fe, and Ca (Traina et al. 1986, Iyamuremye and Dick 1996, Ohno and Crannell 1996). This effect was not observed in cultivated soils at the other 2 sites, probably due to differences in soil chemical and environmental conditions. Further research on the P dynamics of soils from the three sites will be required to explain the differences observed.

Conclusions

We conclude that production of annual agricultural crops on rangelands in tilled systems can deplete soil C and N reserves significantly. The establishment of perennial grasses or legumes on formerly cultivated land can slow, or reverse, the depletion of soil C and N reserves. The stabilization or loss of soil C and N from modified plant communities is affected by climate (soil temperature and moisture) as well as the quantity and chemical characteristics of residues produced by plants. Differences in the total P content of soils under modified plant communities and native rangeland appeared to be related to the initial site preparation rather than experimental treatments or environmental factors.

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Book Reviews

Netting the Sun: A personal Geography of the Oregon Desert. By Melvin R. Adams. 2001. Washington State University Press, Pullman, Washington. 143 p. US$16.95 paper. ISBN 0-87422-236-2.

> *"I began to feel a mysterious attraction to the place as if it were a cathedral, a gallery of sacred art, a primitive testament, a tragedy, a gift, a mystery. I felt as if some cataclysm could happen at any time, that some terrible event or events had happened to sanctify the place."* (Adams, 2001)

This book is mostly a compilation of essays based on Mr. Melvin Adams childhood experience of the Oregon Desert. In telling his experiences he used geography, history, biology, botany, mythology, metrology, and wildlife and other natural resource management. He describes this desert as a place of startling mystery, subdued dander, and beauty. He claims that it is a place to see nature raw, with most of our usual certainty taken from us. To him it is a place where the line between terror and beauty is thin and often crossed.

Mr. Adams claimed that the area is referred to as the *high desert* because the elevation is greater than a mile, with mountain ranges approaching ten thousand feet high. He observes that to the untrained eye this region appears barren and relatively lifeless, a terrain to be endured while traveling from the gambling dens of Nevada to the wet side of Oregon. This region cannot be survived without preparation and attention. *"It is honest in its intention. There is no false sense of security there as one might find in more vegetated regions"* according to Mr. Adams.

In the high desert the sky is immediate. It is place where one can find a heartbeat: rhythms of grass, fluttering of aspen, murmurs of ancient wind. It is a place where he found happiness, where he found voices and signs, some carved by time and winds, some by shamans, the ancient astronomers. He claims that he has found stories in the desert, on rocks and in the alkaline ground.

What makes this book so interesting is that he is telling his story from his experiences. His description is poetic. He reminds me of the great Aldo Leopold, whose writings were also based on his experiences. Adams understands and explains the relationships among the plants and animals, the Indians and their petroglyphs, the elements and their occurrences. For example, he describes *"streaks of rain called virga dance beneath the cloud, flirting with and teasing the dry ground. The effect is not unlike that of a belly dancer in an old Hollywood movie teasing the sultan in his harem tent."* In describing the scene at the Stone Bridge petroglyph site, he claims that the *"shamans in self-portraits appear to dance across the rocks' face as if in a series of drawings for an animated film."*

This is a well-written book that gives you insight about a place that one cannot fully ordinarily observe its complexity. It offers a diversity of natural and human stories from a landscape that appears insignificant to most. It is a book that takes you back home, to a place where your childhood experiences come to life.

This book brought back many memories to me as a kid living in the rural village of Lopinot in the Caribbean islands of Trinidad and Tobago. It recalled my wonderful experiences with nature, the flowing streams with fishes, abundant wildlife, fresh air, the music among the trees and their inhabitants. To some, this was a place where the roads were terrible and amenities did not exist. However, to me it was home, a place that I still look forward to going. Mr. Adams not only reminded me about the greatness of my community but he also showed me that there are other things there I did not see or even know existed. He has helped me to get more out of my childhood experiences back home now than I previously did.

For many of us certain places seem insignificant because we have not experienced it the way others have. We must not think differently about people who cherish rural life and experiences. Instead, we must try to understand their experiences and why they feel the way they do about these special places. Maybe if we all have these feeling about certain place out there in the environment, we may be better poised to protect them and the special meanings they have for us.—*Neemedass Chandool,* Trinidad and Tobago, Washington State University, Pullman, Washington.

Forages. An Introduction to Grassland Agriculture. 6th edition, Vol. 1. 2003. Edited by Robert F. Barnes, C. Jerry Nelson, Michael Collins, and Kenneth J. Moore, with 24 text contributors. Iowa State Press, Ames, Iowa. 556 p. US$79.99 hardbound. ISBN 0-8138-0421-3.

As a student in the late 1970's, I used the third edition of this book in a class on forages at Utah State University. It was more than enough book for the course. *Forages* had plenty of content, a mid–western and eastern emphasis, and a conservative, steam-engine-solid, 2-columned format that you might expect from the Iowa State University Press. It made ponderously agricultural reading in more than a few places, but it had detailed content as a text, and served so well as a reference that the dual-purpose value of the book was indisputable.

Through several subsequent editions, the book has seen significant changes. Three new editors have, over editions 4-6, replaced two earlier ones, and the book was split into 2 volumes for the fifth edition. In the sixth edition, Volume I (reviewed here) is designed as a textbook for undergraduate students, and Volume 2 is designed as a reference.

Forages is organized into 3 main sections. The 10 chapters of Part 1 cover diverse aspects of forages, and include titles such as the *structure and morphology of legumes and other forbs, physiology of forage plants, environmental aspects of forage management,* and *forbs.* The chapter on the structure and morphology of grasses by Lowell Moser and Jerry Nelson is admirably thorough and would be useful to instructors teaching rangeland plants. Part 1 generally shows a stronger tendency toward diverse processes and generalized management than early editions of the book, but Chapters 6-10, entitled *grasses for northern areas, grasses for southern areas, legumes for northern areas, legumes for southern areas,* and *forbs*, contain much of the species-by-species details of management I recall from my undergraduate days.

Part 2, in its 5 chapters, focuses on forage management, and includes chapters on establishment, nutrients and fertilization, integrated pest management, naturalized grassland, and forage improvement and seed production. Chapter 14 on naturalized grassland has some discussion of basic ecology and ecosystems, and is the book's closest approach to rangeland ecology.

Part 3, *forage utilization*, examines forages more from the animal perspective, and includes chapters on forage quality, forage utilization, forage-related animal disorders, hay and silage, and grazing management systems. The discussions here recall more basic animal nutrition, veterinary medicine, and agronomic management than integrated range management science. Following Part 3, *Forages* contains an appendix of common and botanical names of forage plants, a basic glossary, and an index.

If Chapters 6–10 of Part 1 do not provide enough information on individual species, a compendium of common forages between Parts 1 and 2 provides detailed descriptions of individual forage species of the United States. Here the pages are glossy and unnumbered, the photographs and other graphics are in color, and the format is two-columned—a familiar carryover no doubt from the book's earlier editions. Other than the improved modern graphics, this section of *Forages* is definitely reminiscent of the book's past. Each description has a significant section discussing management of each species.

The relocation of the Iowa State University Press within Blackwell Publishing has likely contributed to the generally sleeker format of *Forages*. Gone is the 2-columned text (other than in the compendium of forages discussed above), replaced by a more reader-friendly straight text with more open space. The book even includes occasional inserts containing brief discussions of issues or topics that are related to the discussion, but are sufficiently discrete to be treated as asides. These asides appear occasionally, but the format is still relatively conservative compared with many modern textbooks, some of which begin to resemble pop-up sequences on the Internet. In some way, the book still reflects more Midwestern sensibilities in style and format.

Equally Midwestern, with a touch of *Back East* and *Down South,* is the book's content, reflecting the contributions of authors mostly from east of the Rockies. No matter how thorough the book's coverage of matters related to forages in the East, South and Midwest, it could nonetheless benefit from greater contributions from the West, including a section relating forages to rangelands and to range management science. As it is now, *Forages* is a vivid reminder of the difference between the agronomic character of of forage science, and the diverse elements of range management science.

Within the limits of agronomic science, the technical content of Volume 1 of *Forages* is as detailed as I recall, and will warrant, and require, thorough reading by upper division undergraduate students, or graduate students. Much in the manner of traditional textbooks, questions are included at the end of each chapter as aids to study. Even though Volume 2 is supposed to be a reference, Volume 1 is itself a valuable general reference, and includes numerous, although not burdensome, literature citations. Clearly *Forages'* value as a dual-purpose (text-reference) book is intact even within Volume 1 of the Sixth edition.

Volume 1 of *Forages*, and the courses it is designed for, are valuable links between the agricultural and natural resource sciences, and those links could be further strengthened by bringing more ecology, more range management science, and more of the integrated elements of the Western States into the 7th edition.

Forages has come far since the third edition I used at Utah State University back in the Seventies. It has done so by retaining its best elements, gradually diversifying its content, improving its presentation, and generally but steadily responding to the changing landscape. It is not a trend-setting book, but the avant-garde rarely comes from the heartland. Owing to its detailed character and solid presentation, the book remains the definitive book on forages in the United States. —*David L. Scarnecchia*, Washington State University, Pullman, Washington.

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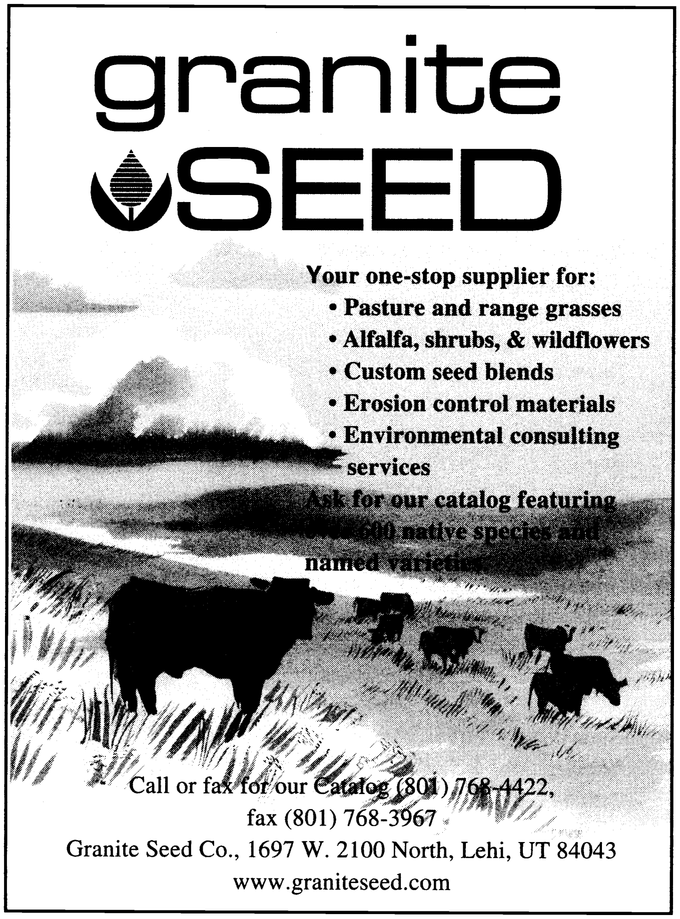

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