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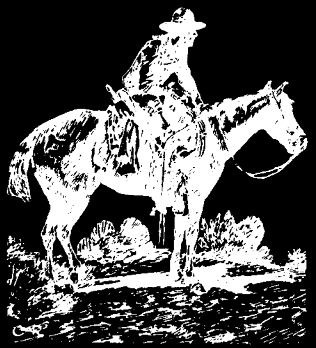

The Trail Boss

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The **Journal of Range Management** serves as a forum for the presentation and discussion of facts, ideas, and philosophies pertaining to the study, management, and use of rangelands and their several resources. Accordingly, all material published herein is signed and reflects the individual views of the authors and is not necessarily an official position of the Society. Manuscripts from any source—nonmembers as well as members—are welcome and will be given every consideration by the editors. Submissions need not be of a technical nature, but should be germane to the broad field of range management. Editorial comment by an individual is also welcome and, subject to acceptance by the editor, will be published as a "Viewpoint."

Economics

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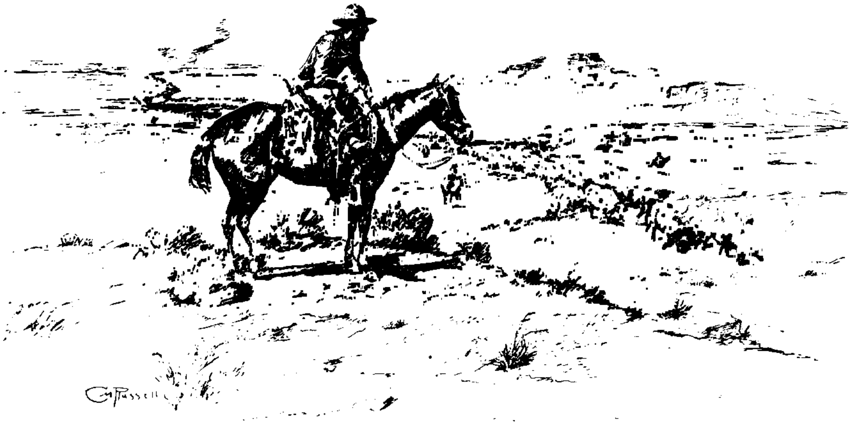

THE TRAIL BOSS

The Society for Range Management, founded in 1948 as the *American Society of Range Management*, is a nonprofit association incorporated under the laws of the State of Wyoming. It is recognized exempt from Federal income tax, as a scientific and educational organization, under the provisions of Section 501(c)(3) of the Internal Revenue Code, and also is classed as a public foundation as described in Section 509(a)(2) of the Code. The name of the Society was changed in 1971 by amendment of the Articles of Incorporation.

The objectives for which the corporation is established are:

—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.

Membership in the Society for Range Management is open to anyone engaged in or interested in any aspect of the study, management, or use of rangelands. Please contact the Executive Vice-President for details.

Contribution Policy

The Society for Range Management may accept donations of real and/or personal property, subject to limitations imposed by State and Federal Law. All donations shall be subject to control by the Board of Directors and their discretion in utilization and application of said donations. However, consideration may be given to the donor's wishes concerning which particular fund account and/or accounts the contribution would be applied to.

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President's Address

Furthering the Range Management Profession

JACK R. MILLER

As I come down to my last official act as President of SRM, it is difficult to decide what to say, or, to find the right words to say it with.

I talked to my wife Jan about what I might use as a theme for this President's Address. Jan has been my loyal supporter, confidant, and secretary through this past year—well, through these past many years. Anyway, we thought it might be good to focus in on things your Society does to further the range management profession. I have heard members, as well as others, ask questions such as, "What does the SRM really do? We know you have good meetings twice a year and the membership really enjoys the close personal relationships and camaraderie. But what does the Society do for the profession?" I will try to address some of the issues that seem important to me.

The SRM has developed a strategic Plan of Work that clearly lays out the mission, goals, and objectives of the Society. An Annual Plan of Work is developed each year that assigns specific objectives for each of the 30 committees, councils, panels, and task groups, as well as the Sections. This planning structure has helped us to place our emphasis where it is most needed and provides better continuity from year to year.

In the next few minutes I will briefly touch on some of the activities that the SRM is engaged in to achieve our mission.

Under the heading of *professional development* I will address several programs that the Society has designed to further development of individual members, as well as the range management profession as a whole.

Continuing Education

As can be seen by the program for this meeting in Corpus Christi, more symposia, work-shops, and training sessions are being held in conjunction with the Annual and Summer meetings. In addition, many Sections are holding such sessions, as well as working with agencies and organizations to offer continuing education opportunities. The responsibility for seeking and taking advantage of these opportunities rests with the individual.

Career Opportunities

The Professional Affairs Committee is working with the Range Science Education Council to analyze trends in resource management to see where future opportunities lie for range-trained professionals. On the other side of the coin is our educational system, continuing to turn out graduates who have the needed skills and are recognized and sought after by potential employers. As we answer these questions we will be in a better position to see improved career opportunities for range managers.

Accreditation

The range Curricula Accreditation Program continues to strive for quality, range management educational programs. There are now 9 colleges with accredited range programs and a 10th is in the mill.

Consultant Certification

This activity of the SRM has great potential for bringing recognition to the importance of range management expertise and improving the quality and reliability of range management services available. There are currently 44 certified range consultants. the Certification Panel is now working with the I&E Committee to develop an excellent informational brochure.

Monitoring Guideline

The Excellence in Range Management Committee, formerly the Producer Affairs Committee, has, as one of its objectives, to develop a statement regarding the importance of range resource monitoring and some basic guides to assist users in resource monitoring.

Range Cover Type

At the request of several Federal agencies, SRM is moving ahead with an effort to identify and describe major range cover types in the U.S. This undertaking is being coordinated by Tom Shiflet and will involve many of our members. The product will be a document similar to Forest Cover Types that has been in use for several years. This may be expanded to include Canada and Mexico.

Publications

The *Journal of Range Management* and *Rangelands* are quality, professional publications. The Society also produces a number of other publications pertaining to management of range resources. One example is the *Glossary of Terms*, which has recently been updated and will soon be available. A new item is the long-awaited, *35-Year Index* of *JRM* articles which is now available. If you don't have yours, be sure to get hold of Pete, or one of the Denver staff, and purchase a copy.

History

SRM is 40 years old this year. It was built and has survived on the hard work and dedication of many people. Many of you in this room are charter members. These 40 years are rich with the happenings that make a society like ours grow. Some happy, some not, but all part of our growth. The History and Archives Committee works to preserve this heritage. A small group of dedicated members recently spent many hours pulling together and writing a summary of the development of the SRM. This, too, is now available.

Student Activities

Certainly young people are the future of our profession and our organization. The SRM carries out a number of student activities that help to attract young people into the profession and start them off on a career. You have seen examples of that today. We are proud of these young people and the members of the Student Activities Committee that work with them.

Awards

It is important that recognition be given for a job well done. Our awards program is designed to do that. The hard part is selecting the most deserving people from among the many quali-

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Presented 24 February 1988 at the 41st Annual Meeting of the Society for Range Management, Corpus Christi, Texas. Jack Miller was 1987 president of the Society for Range Management.

fied. Everyone has a part to play in nominating award candidates. The Awards Committee can screen and process nominations, but they can't make them. We have had a number of new awards in recent years with the Chapline Awards, and proposals for others are being considered.

Another main heading of activities that SRM is involved in is the area of *public outreach.* The general public, and even many natural resources and environmental groups, do not understand or appreciate the importance of range resources. Information that others get regarding range resources is often incomplete or misleading and tends to create false impressions.

SRM is doing a number of things to establish a leadership role in range management and provide the public with factual, understandable information.

Washington, D.C. Liaison

Clare Hendee filled this role for many years, using his own resources for the most part. Two years ago the Board made a commitment to provide additional funding to strengthen our presence in the United States' Capitol. Ray Housley, with assistance from George Lea, is now doing that job and doing it well. We are being informed of pertinent activities at the national level and becoming increasingly recognized as a professional society. I hope you are reading the Capital Corral section in *Rangelands.* It gives the best, quick insight into the happenings concerning natural resources, particularly range resources, that I've seen.

Public Outreach Position

At the time the board made the decisions to provide additional funding to the Washington, D.C., Liaison, there was a second proposal from the I&E Committee for a Public Relations position on the Denver staff. We couldn't afford both, and it was a tough decision. We decided to forego the public relations position for the time being. However, effort continued and, I am happy to announce, we established a position half-time in the Denver office last month. The person filling this position is Jerry Schwien, a public affairs specialist with the SCS in Denver. Jerry will be working half-time in the Denver office under the supervision of Pete Jackson. His salary is funded by SCS with some other agencies helping in other areas.

Denver Office

This year, after several years of looking, SRM purchased and moved into a new office. The building is not new, but it is a classic that was originally built as a residence for Lieutenant Governors of Colorado. It is a beautiful building and is a fine headquarters for our professional society. An open house, last month, was sponsored by the Colorado Section. It attracted a large number of people from the Denver area and acquainted them with our new location. The Colorado Section is also working to establish a plantation at the office with representative State Grasses from all the states that have them. In the meantime, the old office building is completely rented and will go up for sale when the commercial real estate market in Denver looks right.

National Range Conference

Do you remember the National Range Conference that was held in Oklahoma City? It was the first conference of that type concerning range resources and resulted in an extensive plan of action to further objectives of good range management. SRM was given the lead role in a number of action items and these have been disseminated to various committees for action. There will probably be another national range conference in the not-too-distant future and SRM will be right in the middle of it.

Conservation Reserve Program

The CRP has potential to have major effect on management of range resources and range-related industry. Recognizing this, the Colorado Section jumped to the forefront in sponsoring a Conservation Reserve Program Symposium in Denver. The symposium was an outstanding success and attracted a large turn-out, including the Secretary of Agriculture and heads of two resources agencies as speakers. During a panel discussion, Wilson Scaling, Chief of the SCS, outlined some challenges to SRM on how we might be more effective in promoting range management, particularly in relation to the CRP. In response to that, we have appointed a CRP Task Group under the direction of Harold Goetz, head of the Range Department at CSU, to consider these challenges and propose a plan of action.

Success in Range Management

In recent years we have seen an emergence of public interest in management of range resources. Unfortunately, this is often manifested in a negative light giving the impression that a poor job has been done of managing our range resources. Prompted by initiative from Stan Tixier, Regional Forester with the USFS, effort is being made to make visible more of the many success stories in improving range resources. One of the concurrent sessions for this meeting is dedicated to that. I believe this is a bandwagon more of us should jump on.

Range Condition Assessment

As I just mentioned, we have seen a number of articles critical of what is happening to our range resources. Quite often these articles make references to range condition reports prepared by agencies to support an argument that the range is going to hell in a hand basket. As professionals, we recognize there are certainly examples of current mismanagement of range that are in need of correction, but by and large, condition of rangeland in the U.S. has improved over the past 50–60 years.

If that is the case, available range condition reports must be misleading, or at least, subject to misinterpretation. I believe SRM, the leading professional organization concerning range management, has a role to play in coordination with the agencies to interpret range assessment data and provide accurate and understandable information to the public on what has happened to our range resources over the years and what is happening now.

We have a sub-committee of the Public Affairs Committee working on that.

Much of what I have said so far has been in reference to the United States or at least the North American Continent. Let's not forget, we are an international organization. We have members in 48 countries, but, that in itself, does not make us an effective international organization. What are we doing to promote proper management of range resources on an international scale? The International Affairs Committee puts out an International Range Newsletter which is intended to effect a networking between countries and encourage activity in range management.

SRM supports the International Rangeland Congress Continuing Committee which plays the lead in scheduling and organizing the International Rangeland Congress. So far, the IRC has been held in United States and Australia—one is scheduled for later this year in India. This is a fascinating part of the world and I hope there will be a good representation of SRM members. Future IRC's? I have heard mention of locations such as Mexico, Africa, and China.

We support formation of additional Sections of SRM in other countries or additional range organizations. Pete Jackson recently attended a meeting of the Third Rangeland Congress of Mexico in Durango, Mexico. There, the first steps were taken to form a Mexican Society for Range Management. We feel each country should consider their own situation to determine what is best. If the economic and political climate is such that a country can be more effective with their own society, we support that. If Mexico goes that way, we would like to continue a strong partnership, retain their activity in our Society and, hopefully, maintain a Mexico Section.

(continued on page 117)

Arthropod predation of black grass bugs (Hemiptera: Miridae) in Utah ranges

JAIME E. ARAYA AND B. AUSTIN HAWS

Abstract

The predation by selected arthropod predators on immature and adult black grass bugs (BGB), *Labops hesperius* and *Irbisia brachycera*, on Utah ranges was investigated. Adult *Nabis alternatus* was found to be the most important predator of BGB; this species is particularly abundant in early spring and was observed preying on BGB both in the field and in laboratory feeding tests. Immature nabids consumed the bugs but preyed mostly on leafhoppers, smaller plant bug nymphs, and other immature nabids. *Nabis vanduzeei* showed potential as a predator of adult BGB in the laboratory feeding tests. Spiders were important predators of BGB. Based on predation of BGB in field and laboratory studies, the spiders observed were ranked as follows from greatest to least importance as predators: *Xysticus cunctator, Misumenops lepidus, Tibellus* sp. (Thomisidae), *Castianeira* sp. (Clubionidae), and *Tetragnatha* sp. (Araneidae). Spiders attacked any prey of a size similar to themselves, but they also preyed on beneficial arthropods, including nabids and other spiders.

Key Words: wheatgrass, Lycosidae, *Metepeira foxi, Paradecerla formicina*, wolfspiders

Large areas of rangelands in Utah and other western states have been seeded to introduced wheatgrasses (*Agropyron* sp.) which are infested with the univoltine black grass bugs (BGB) *Labops hesperius* Uhler and *Irbisia brachycera* Uhler (Hemiptera: Miridae) (Hewitt et al. 1974, Rogler & Lorenz 1983). The BGB hatch as soon as the winter snow melts and begin to feed on and damage grasses during the critical early spring stage of plant growth (Brewer et al. 1979). The damaged grasses develop a yellow to whitish mottling marked with small, black fecal spots. Heavily affected grasses may eventually become completely dry. Severely damaged plants seem to be unattractive to livestock (Haws et al. 1973, Higgins et al. 1977, Malechek et al. 1977).

The major BGB species in Utah appears to be *L. hesperius*, but *L. hirtus* Knight and *L. utahensis* Knowlton are also important in certain areas (Knowlton 1945, Haws et al. 1973, Hewitt et al. 1974). Details on the biology of *L. hesperius* can be found in the review by Araya (1982). Another important BGB, *I. brachycera*, has apparently been responsible for much of the damage formerly attributed to *Labops* (Hewitt et al. 1974). BGB are not usually present in large numbers on native grasses (Higgins et al. 1977) or in areas intermixed with native plants (Haws et al. 1973), probably in part because these ranges provide a good habitat for insect-eating arthropods.

The management of crop pests through biological and integrated control methods requires an understanding of the complex interactions between the pests and beneficial insects (Smith et al. 1976). While beneficial arthropods are essential elements in integrated pest control, very little is known concerning their relative efficiency in controlling pest species (Wilson and Gutierrez 1980). Information about predators of insects in rangeland grasses is particularly scarce.

Most predators are polyphagous, thus a direct predator-prey relationship is difficult to ascertain. Knowledge of the seasonal abundance of predaceous arthropods is helpful in defining their roles in regulating insect pests. This information is essential for developing effective insect pest management programs (Shepard et al. 1974). Many predators can be observed in rangelands, but the effectiveness of each species is difficult to evaluate in field studies. Cage tests in the greenhouse might be a preliminary step in establishing an index of predator efficiency against each prey species. Such an index can be used for planning integrated control programs (Tamaki and Weeks 1972).

The objectives of this study were: (1) To identify major potential invertebrate predators of BGB in selected Utah ranges, and (2) To compare predation by adult and immature invertebrate predators on selected range insects under laboratory conditions.

Materials and Methods

These studies were conducted in BGB-infested rangelands near Porterville, Morgan Co., Utah; Logan, Cache Co., Utah; Hodge Creek, Logan Canyon, Cache Co., Utah; and the wheatgrass ranges around the Alpine Cabin of the Intermountain Research Station, Ephraim Canyon, Sanpete Co., Utah. A brief description of the study sites appears in Table 1. Laboratory studies were conducted in the Range Entomology Laboratory, Department of Biology, Utah State University, Logan.

Procedures for Objective 1

A 38.1-cm diameter sweep net was used to collect insects and spiders periodically during the growing seasons of 1981 and 1982 from selected grasslands with BGB (Table 1). Litter sampling on the same dates and fields was helpful particularly in providing immature BGB specimens. Pitfall traps helped in identifying the species of arthropods present, but were considered unreliable because of the different behavior responses they induced on different species of arthropods, as evident in preliminary studies, and because they provided mostly dead or damaged specimens. Quantitative data on arthropod abundance is described by Araya (1982).

Procedures for Objective 2

Live BGB and insect predators were separated from the material collected with the sweep net and from the litter sampled (particularly for immature BGB) by using an aspirator, a small hair brush, or grass leaves or stems that some insects readily grasp. Spiders were separated with forceps. Three studies were designed.

Studies of Predation with One Species of Prey Per Predator, Growing Season of 1981

Ten adults of either *L. hesperius* or *I. brachycera* were caged with one adult predator of each of the selected predator species (the most abundant in the field), in transparent plastic cylinders 25 cm high and 9 cm diameter. Each cylinder was covered with a screen lid and had a vial holding a small clump of live wheatgrass (*Agropyron* sp.) on the bottom on which the BGB could feed (Araya 1982). BGB mortality was recorded every 2 days, and the dead insects were replaced with live ones. There were at least 5 replica-

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The contributions of our colleague entomologists Eric Coombs and Roy Meadows during these studies, the identification of spider species by Dr. Eric Zurcher, Utah State Univ., and Dr. W.J. Gersh, Univ. of Arizona, and of ants by Dr. George C. Wheeler, San Antonio, Texas, are greatly appreciated.

Manuscript accepted 29 October 1987.

Table 1. Some invertebrate predators of black grass bugs collected from selected Utah rangelands during the 1981 and 1982 growing seasons.

Predators	Localities[1]	1981	1982
Insects:			
-*Nabis alternatus*	P	———— May 3, 17, 28 June 3, 10	Apr. 14, 22, 28 May 4, 6, 10, 14, 21, 27, June 2, 14, 21, 28
	H	June 20, July 2	————
	A	July 30	————
-*Nabis vanduzeei*	P	May 12, 17, 28, June 3, 10	May 27, June 21, 28
	L	June 17	————
	A	July 30	————
-*Nabid nymphs*	P	———— ————	May 21, 27, June 2, 14, 21, 28
-*Paradecerla formicina*	P	May 28	————
	A	July 29, Aug. 6	————
Spiders:			
-*Xysticus cunctator*	P	May 12, 17, 28, June 5, 12, 18	May 21, 27, June 2, 14, 21, 28
	H	June 20, July 12	————
	L	June 21, July 2	————
	A	June 25	————
-*Xysticus benefactor*[2]	P	June 18	————
-*Misumenops lepidus*	P	May 8, 18, June 18	May 27, June 2, 28
	L	July 1	————
	A	June 25	————
-*Tibellus* sp. (either *T. oblongus* or *T. chamberlini*)	P	June 18	————
	L	June 14, 21	————
-*Thanathus* sp.	P	————	May 2, 10, 14, 21, 27
-*Tetragnatha* sp.	P	June 5, 12, 18	May 27
	H	June 20	————
	L	June 14	————
	A	June 27	————
-*Metepeira foxi*	P	June 18	Apr. 14, 27, May 4, 27, June 2
-*Castianeira* sp.	P	May 26, June 9	Apr. 14, May 4, 10, 27
	H	July 16	
	L	July 5	
	A	June 25	

[1] P = Porterville, Morgan Co., UT (wheatgrass monoculture on about 1,600 m elevation hillside fields. L = Logan (semi urban field with diverse grasses and forbs, about 1,400 m elevation), Cache Co, UT. H = Hodge Creek, Logan Canyon, Cache Co., UT (a field patch surrounded by shrub and tree species, on a creek about 2,000 m elevation). A = Fields around the the Alpine Cabin of the Intermountain Res. Exp. Sta., Ephraim Canyon, Sanpete Co., UT.

[2] One male specimen, identified by Dr. W.J. Gersh, Univ. of Arizona.

tions of 10-day long tests for each individual predator tested, although more replications were used for some species. BGB natural mortality was evaluated from control cylinders containing no predators. Ten-day long tests were repeated at different times of the growing season to test for consistency of the results, which was verified since these replications were not significantly different.

Studies of Predation with One Species of Prey Per Predator, Growing Season of 1982

Five-day experiments similar to those of 1981 were conducted in 1982, but the plastic cylinders were replaced with 5 cm diameter Petri dishes lined with moistened filter paper. The Petri dishes facilitated handling of the predators and mortality data were more rapidly collected, compared to the 10-cm cylinders used the previous year. Each Petri dish contained a grass clump (*Poa* sp., a suitable host plant for BGB, as seen in preliminary observations), that was tied with filter paper around the base to keep the grass fresh. Filter paper liners and food were replaced every 48 h to reduce mortality due to waste accumulations. The number of adult or immature BGB per predator and replication was increased from 10 to 20. Mortality of BGB was recorded every 24 h and the dead prey were replaced with live insects. At least 5 replications of 5-day tests per predator were used in tests with immature BGB. Five replications were always used in tests with adult BGB.

Because of the varying number of replications, the differences in BGB mortality detected through ANOVA in 1981 (Table 2), and in 1982 with immature prey (Table 3), were compared using the "t" distribution method between means of non-paired samples (LeClerg et al. 1962, Araya 1982). Significant differences in mortality of adult BGB in 1982 detected in an ANOVA were separated using the Duncan multiple range test (Duncan 1955).

Table 2. Mean numbers of dead adult *Labops hesperius* and *Irbisia brachycera* after exposure to selected predators, in numbers of prey dead each 48 h from a total of ten individuals per cyclinder and predator in 1981 (means of ten-day long feeding trials).

Treatments (predators)	Numbers of dead prey	
	Labops	*Irbisia*
-*Xysticus cunctator*	6.03a	6.14 b
-*Tibellus* sp.	5.92a	....
-Tetragnatha sp.	4.24 b	6.10 b
-*Misumenops lepidus*	3.80 bc	5.96 b
-*Nabis vanduzeei*	3.25 cd	7.15a
-*Castianeira* sp.	3.00 cd	5.64 b
-*Nabis alternatus*	2.67 d	5.72 b
-Control	0.94 e	4.10 c

Results in the same column followed by different letters are significantly different ($P<0.05$), according to tests of significance utilizing the "t" distribution between means of non-paired samples with different numbers of observations (LeClerg et al. 1962, Araya 1982).

Studies of Predator Preference

Whole samples of the arthropods collected periodically with the

Table 3. Mean numbers of dead immature and adult *Labops hesperius* and *Irbisia brachycera* after exposure to selected predators, in numbers of prey dead each 24 h from a total of 20 individuals per Petri dish and predator in 1982 (means of five-day long feeding trials).

		Numbers of dead prey			
		3rd-4th instar nymphs[1]		Adults[2]	
Treatments (predators)	Stage of development	*Labops*	*Irbisia*	*Labops*	*Irbisia*
-*Nabis alternatus*	Adults	5.26a	4.09a	3.56a	4.28a
-*Xysticus cunctator*	Adults	...	...	...	3.12 b
-*Misumenops lepidus*	3rd instar	...	...	3.44a	2.28 cd
-Nabid nymphs	3rd instar	1.76 b	...	3.04ab	2.56 bc
-Wolf spiders (Lycosidae)	Adults	1.36 bc	0.92 c	...	...
-*Castianeira* sp.	4st instar	1.20 bc	2.08 b	...	...
-*Tetragnatha* sp.	3rd instar	1.12 bc	...	...	2.44 cd
-*Formica* spp.	Adults	1.07 bc	1.09 c	...	...
-*Tanathus* sp.	Adults	0.76 c	2.12 b	2.44 bc	1.96 cd
-Control	....	0.90 c	0.90 c	1.92 c	1.88 d

[1] Results in the same column followed by different letters are significantly different ($P<0.05$), according to tests of significance utilizing the "t" distribution between means of non-paired samples with different numbers of observations (LeClerg et al. 1962, Araya 1982).

[2] Results in the same column followed by different letters are significantly different ($P<0.05$), according to Duncan multiple range tests (Duncan 1955).

sweep net from the selected Utah ranges infested with BGB (Table 1) were put into transparent acrylic cages 59 × 30 × 30 cm lined with moistened filter paper to avoid dehydration and containing fresh grasses and forbs. All the arthropod specimens in the cages that were observed to be involved in a predatory activity (e.g., specimens in the act of preying or being preyed upon) were collected and identified (Araya 1982).

Results and Discussion

Nabids and spiders were present throughout the study areas during 1981–1982 (Table 1). Adult *Nabis alternatus* Parshley overwinter and appear early in the season (Taylor 1949). In early spring, adult *N. alternatus* which have successfully overwintered are practically the only enemies of the early stages of BGB, and help reduce *Labops* populations at the time of the year when they damage the host plants most (Haws et al. 1973, Higgins et al. 1977, Brewer et al. 1979). *Nabis vanduzeei* Kirk was also collected and was particularly common near Porterville in June of 1982. The predatory mirid *Paradecerla formicina* (Parshley) was abundant in 1981 on the elevated ranges in Ephraim Canyon. Thomisids were the most important spiders preying on BGB, *Xysticus cunctator* Thorell in particular, because of its abundance and active predation on adult BGB (Araya 1982). *Xysticus* spp. are very quiet spiders and do not walk when disturbed (Kaston 1972). Second in abundance in 1981 appeared to be *Misumenops lepidus* Mceler (Hentz). *Tibellus* sp., another 'crab spider' fairly common in bushes and tall grass (Kaston 1972), was extremely mobile and difficult to handle, but it was observed preying on adult BGB in the field study sites. *Misumenops* showed an intermediate level of mobility between those of *Xysticus* and *Tibellus*. *Thanatus* sp., another thomisid common on grasses (Kaston 1972), was collected during May of 1982 near Porterville.

Tetragnatha sp. spiders (Araneidae) were commonly collected from grasses in 1981, but were less abundant in 1982. They characteristically waited for their prey hanging from their webs with their long anterior 2 pairs of legs extended in front of their slender and elongated bodies. *Castianeira* sp. (Clubionidae) was fairly common in all fields examined, but its populations were composed mostly of immature stages. *Metepeira foxi* Gertsch & Ivie (Araneidae) was collected in small numbers since it prefers areas with shrubs rather than open grasslands. The majority of spiders in Utah ranges overwinter as immatures. They become active and develop in the spring, maturing into adults during the summer (Dr. Eric Zurcher, Utah State Univ., personal communications, 1982). Most spiders collected in this study during early spring were 3rd instar spiderlings. The specimens collected thereafter were larger and more developed. The exception were 'wolf spiders' (Lycosidae). Many mature wolf spiders were observed near Porterville early in both years, but they were difficult to handle. Lycosids were not seen preying on BGB in the field, but because of their abundance they were included in the predation tests of 1982. However, they did not kill BGB in the laboratory feeding tests. Further studies are required to determine their prey during early spring. Some other spiders collected were not included in the feeding studies because of their scarcity in the field.

Besides the predation on BGB, *M. lepidus, Tetragnatha,* and *Castianeira* were observed occasionally preying on leafhoppers in the field. Leafhoppers were very common insects on the rangelands studies. *Xysticus cunctator* was also observed preying on nabids, grasshopper nymphs, and on its own species. Remains of leafhoppers and small flies were found occasionally in the field hanging from the silky traps of *Tetragnatha, Castianeira,* and *Thanatus*.

Tables 2 and 3 summarize the mean mortalities of BGB by selected predators in the 1981–1982 laboratory tests. Spiders, *X. cunctator* and *Tibellus* in particular, were effective predators of *L. hesperius*. They preyed significantly more on BGB than did the other predators in the 1981 laboratory tests. Following in predatory activity were *Tetragnatha* and *M. lepidus*. The third most effective group of predators were the two nabid species and *Castianeira*. This spider is relatively slow compared to BGB, and probably prefers smaller prey, as it was observed preying on leafhoppers and small plant bugs in the field. As opportunistic predators, spiders will attack any prey easy to catch and handle (Lincoln et al. 1967, Howell and Pienkowski 1970), feeding on pests but also on beneficial insects (Whitcomb and Bell 1964).

Irbisia had a higher natural mortality than *Labops*. This might be attributed in part to the grass (*Poa* sp.) fed to the BGB. *Irbisia* may prefer other grasses (Haws et al. 1973). The relatively greater predation on *Labops* perhaps reflected the greater mobility of *Irbisia* and their ability to escape from predators in the field. Unlike *Labops*, the greatest mortality of *Irbisia* resulted from their exposure to *N. vanduzeei* (Table 2). All other predators tested consumed significantly fewer BGB than this nabid, but they had similar predation levels among themselves. Even though a given predator may be very efficient individually, it may have little impact on a pest if its own field population is small or reduced or if it prefers smaller prey (Wilson and Gutierrez 1980), and also if it is attracted to prey other than the pest species, as reported for *Nabis* spp. and *Geocoris* spp. (Knowlton 1943, 1944, 1949, Whitcomb and Bell 1964, van den Bosch and Hagen 1966, Eveleens et al. 1973).

The list of predators tested in 1982 (Table 3) was different from that of 1981. The 1982 growing season was delayed because of the severe winter, and spiders collected in May were mostly immatures (except *Thanatus* and wolf spiders). *Nabis alternatus,* especially adults, were the most significant predators of immature and adult BGB both in the laboratory and from field observations, confirming their value during early spring, the most critical time for infested grasslands (Brewer et al. 1979). Second in predation on *Irbisia* was *X. cunctator,* followed by immature nabids. Other arthropods tested failed to increase the mortality of immature *Labops* compared to the controls. With the exception of *Castianeira* on immature *Irbisia,* immature spiders tested appeared not to be effective predators of immature BGB, probably because of their smaller size. Size is a determinant factor in predation (Howell and Pienkowski 1970, Wilson and Gutierrez 1980). In the 1982 laboratory feeding tests, *Xysticus cunctator* and *M. lepidus* preyed effectively on adult BGB. *Thanatus* did not increase the mortality of immature or adult BGB. This is a very quiet spider and appeared to prey on flying insects such as flies or leafhoppers. However, remains of BGB with signs of having being preyed on where commonly observed on their irregular webs. Further studies are needed to clarify the predatory activity of *Thanatus* and wolf spiders. Lycosids may have not preyed upon immature BGB because of behavioral changes due to confinement in the Petri dishes. These fast moving spiders tried constantly to escape from the dishes. To avoid this problem, larger containers simulating more closely natural grassland conditions should be used in further studies.

Ants (mainly *Formica neogagates* Emery, but we collected also some specimens of *F. subsericea* Say) appeared to be only field scavengers and did not prey upon BGB. Scavenging by adult *Labops* was also observed. After adult *Labops* were killed by *N. alternatus* during the 1982 tests, some produced exudates, possibly because of the action of digestive enzymes and the humid environment in the Petri dishes. Some adult *Labops* were observed momentarily tasting the exudate from the dead prey, continuing thereafter with their normal feeding on the grass clumps and sucking water from the moist filter paper. Nabids were observed occasionally inserting their beaks onto the grass both in the field and in the laboratory, apparently tasting the grass sap.

From our field observations and the results of the laboratory feeding tests, we concluded that several beneficial arthropods preyed actively upon BGB. Among them, nabids and several spider species caused significant laboratory mortality of BGB. Further studies on predation (and parasitism) of BGB are needed in order to clarify the relationships between the different components of rangeland ecosystems and to help explain the annual fluctuation in BGB population, in order to preserve these delicate environments, and to provide strong scientific basis for the development of sound integrated pest management systems for range pastures.

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Longevity of harvester ant colonies in southern Idaho

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Abstract

Harvester ant colonies (*Pogonomyrmex owyheei* Cole) in southern Idaho were monitored periodically for 9 years. Mortality rates indicate that established colonies live 14–30 years ($\bar{x} = 17$). Mounds were commonly reactivated after the death of an old colony; consequently, some may be utilized for many decades. Clearings with active mounds showed almost no change after 9 years of observations while those without active mounds were rapidly filled by annual herbs and then gradually by perennial shrubs. Harvester ants are clearly a very persistent component of cold desert shrub communities.

Key Words: *Pogonomyrmex*, persistence, survivorship, mounds, clearings

Pogonomyrmex harvester ants are conspicuous features of rangelands throughout much of western North America. This is especially true of the northwest species, *Pogonomyrmex owyheei* Cole, which constructs distinctive gravel-covered mounds surrounded by large clearings. Harvester ants have been considered pests (Crowell 1963, List 1954) because they occasionally clear up to 10% of range area (Sharp and Barr 1960, Willard and Crowell 1965). Fortunately, the percentage of land cleared is generally much less (Sneva 1979, Rogers and Lavigne 1974) and the damage is largely compensated by increased vegetational production around clearing perimeters (Wight and Nichols 1966, Rogers and Lavigne 1974).

Colonies construct clearings by systematically clipping off plants emerging too near their mounds (Clark and Comanor 1975). This behavior exposes the mounds to direct sunlight earlier in the morning when it is most beneficial for thermoregulation (Seeley and Heinrich 1981). Clearings may also benefit the colony by speeding transit of foragers and eliminating hiding places for harvester ant predators (Clark and Comanor 1975).

Earlier observations indicated that harvester ant mounds and clearings changed little from year to year (Sharp and Barr 1960), and that the colonies themselves may be very long-lived (Michener 1942, Wildermuth and Davis 1931). In order to investigate the longevity of harvester ant colonies, we monitored approximately 120 mounds over a 9-year period, 1977–1986.

Methods

This study was undertaken in Raft River Valley, Ida., as part of a larger environmental monitoring program (Jorgensen 1979). All plots were located in mixed sagebrush *(Artemisia tridentata wyomingensis)* and greasewood *(Sarcobatus vermiculatus)* plant associations. These shrubs together with *Lepidium perfoliatum, Sitanion hystrix, Descurainia richardsonii, Bromus tectorum* and *Ceratoides lanata* accounted for >95% of the vegetation. Rainfall averaged about 24 cm (9.5 inches) in 1977 and 1978. Plots were located on the lower parts of alluvial gravel deposits interspersed with intermittent drainage streams. Livestock grazing was generally moderate from November to May, leaving range condition fair but needing improvement (Burley District, BLM).

We initially mapped *P. owyheei* mounds at 3 small plots (0.25 ha) and 1 large plot (2.72 ha, Fig. 1) in 1977. Mounds and clearings in 2 of the small plots (A and B) were measured and checked for activity several times a year during 1977–1980 and again in 1986. Colonies at the third small plot (removal) were poisoned with Diazinon (1977) to determine how rapidly an area was reinvaded after the inhabitants died. Mounds at the main plot (Fig. 1) were mapped and checked for activity in 1977, 1979, partially in 1980, and again in 1986. These mounds were assigned to size classes according to their diameters: small (<30 cm), medium (30–60 cm), and large (>60 cm). Mound activity was determined either by the presence of ants or fresh piles of chaff deposited near the mound. If a mound appeared to be inactive, we dug into the mound to confirm the absence of ants; this avoided the possibility that a mound would be declared inactive simply because the colony had not been foraging recently. Vegetational cover for the main plot and plots A and B was 18%, 31%, and 15%, respectively.

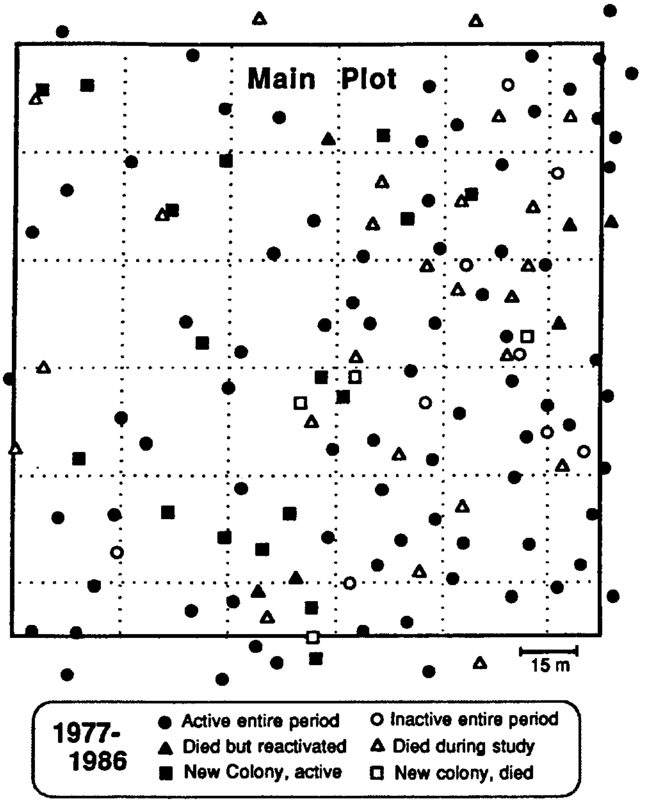

Fig. 1. *Distribution and activity of* Pogonomyrmex owyheei *mounds on the main plot from 1977–1986. Closed symbols indicate active mounds in 1986 and open symbols indicate the inactive ones.*

Results

Persistence of Mounds

Mound densities on our study plots averaged 40/ha with about 4% of the area included in clearings. The total number of active

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mounds remained relatively stable at 122, 128, and 119 mounds in 1977, 1979, and 1986, respectively. Of the original 122 active mounds, 80% (97 mounds) were still active after the 9 years (see Figure 1 for activity changes on the main plot). At least 6 of these mounds were temporarily abandoned and then reactivated by a new colony. A total of at least 36 colonies died during the study and 30 new colonies were established. Six mounds remained recognizable even after more than 9 years of inactivity. Mortality rates appeared to be associated with mound size. Approximately 50% of small, 30% of medium, and 25% of large mounds were abandoned between 1977 and 1986. This relationship suggests that colonies in small mounds are shorter lived, but this could also result because smaller mounds were less likely to be reactivated during the 5-year interval when the plots were not monitored (1981–1985).

Colony Longevity

Longevity was calculated by dividing the number of colonies alive over a specific time period by the number which died (Table 1). For example, 23 mounds on plots A and B were monitored for 3 years. During this time, we accumulated 61 active colony years and observed 4 deaths; thus the estimated longevity was 15 years. We also checked the activity of 68 colonies at the main plot for 1 year; 5 colonies died during this year producing an estimate of 14 years. Sharp and Barr (1960) monitored the activity of colonies over 2 years at study sites in the same valley. Their 3 sites were located in shadscale *(Atriplex confertifolia)*, saltsage *(Atriplex tridentata)*, and "depleted" or heavily foraged saltsage. Longevity estimates calculated from their data ranged from 14–30 years (Table 1).

Table 1. Estimated longevity of harvester ant colonies *(Pogonomyrmex owyheei)* in the Raft River Valley of southern Idaho.

Vegetation	Sample Dates	$\bar{x}$ Number of Mounds	Mound Years	Number of Deaths	Longevity in Years
Sagebrush and Greasewood					
Plots A & B	1977–80	20	61	4	15
Main Plot	1979–80	68	68	5	14
Shadscale	1956–58	61	121	4	30*
Saltsage	1956–58	28	56	2	28*
Depleted Saltsage	1956–58	112	223	16	14*
		Total	529	31	17

*Calculated from Sharp and Barr (1960)

The longevity estimates in Table 1 require the satisfaction of 3 assumptions: (1) colonies died rather than emigrated, (2) sampling frequency was sufficient to detect mortality, and (3) populations retained stable age-distributions during the study. The assumption that inactive colonies died rather than emigrated is fairly robust and acceptable. Unlike other members of its genus (Carlson and Gentry 1973, Van Pelt 1976), mature *P. owyheei* colonies rarely emigrate unless they are poisoned or severely disturbed (Willard and Crowell 1965). In 4 years of intensive study, we observed only 1 naturally occurring emigration, and it was eventually aborted. The second assumption, that sampling frequency was sufficient to detect mortality, also seems to be satisfied. Plots A and B were checked at least monthly (1977–1980) so it is highly unlikely that colony death and reestablishment could have occurred unnoticed. Other plots were surveyed once a year, but this was probably also sufficient because recolonization by founding queens could occur only in August and at least a year would be required before an incipient colony grew enough to be noticeable. Also, successful "yearling" colonies were very uncommon. The third assumption, a stable age distribution, is more questionable because we could not determine how long colonies had been at the plots prior to sampling. The main problem would be if our study populations had been founded in waves. Thus, if we sampled soon after a founding wave, the longevity estimate would have been too high, while if we sampled late in the cycle, it would have been too low. Problems with this assumption may account for some of the variation in Table 1; however, the fact that all 5 estimates exceed 10 years supports the conclusion that harvester ant colonies are very long-lived.

Mound Dimensions

Seventeen of the 22 mounds on plots A and B were active throughout the study. The average diameter of these mounds changed little during the course of our study; however, mound heights increased 20–50% between 1977–79 and 1986 (Fig. 2, repeated measures ANOVA, Scheffé F-test, $p<0.05$). This increase could be due to either a gradual accumulation of rocks over the years, or a general increase in colony size, perhaps as a result of almost 5 years of above-normal precipitation in the valley. Active mounds at the main plot also seemed to increase in size, but 70% did not change enough to switch size classes. Five mounds remained small throughout the study. Twelve mounds grew from small to medium, and another 13 from medium to large. Two mounds grew all the way from small to large. The only mounds which lost size were those in which the colony died.

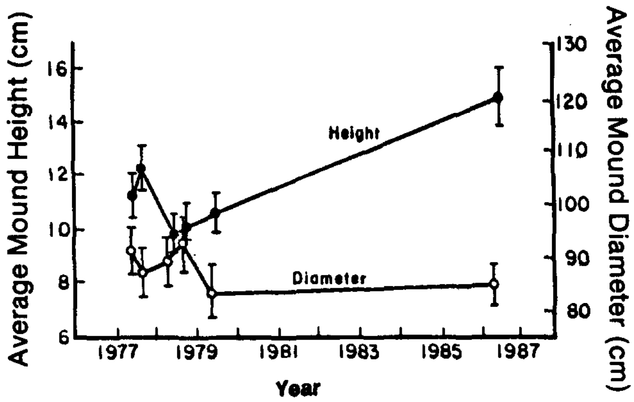

Fig. 2. *Average changes in* Pogonomyrmex owyheei *mound height and diameter of 17 mounds from 1977 to 1986. Standard errors are shown for each point.*

Clearings

After 9 years, the size and shape of clearings on plots A and B changed very little. In fact, comparison of photographs taken in 1977 and 1986 revealed a remarkable lack of change (Fig. 3A). Many dead sticks and branches were still in the same locations they had been 9 years earlier. Most bushes were even the same general shape and size; a fact not too surprising considering sagebrush is often very long lived and slow growing (Ferguson 1964). The diameters of the clearings, however, averaged about 8% smaller in 1986 than in 1977-1979 (3.5±1.1 m versus 3.8±1.1 m; $p<0.05$, Scheffé F-test). This change may reflect increased growth of vegetation during a period of wet years, or it may simply indicate that clearings are often irregular and measuring them is difficult to standardize.

Removal Plot

The removal plot initially contained 18 active mounds. The poison treatment in 1977 was not completely effective. In 1978, almost half of the mounds were still active, albeit at rather low rates. The queens of most colonies had probably been killed the previous year, but workers in the pupal stage managed to survive. When we surveyed the plot in 1986, only 5 of the 18 mounds were still active, and 3 of these showed distinct signs of having been reactivated based on the degenerated condition of the mound and surrounding clearing. No new mounds were found in the plot. The 13 inactive mounds were still plainly visible after 8 years, but they

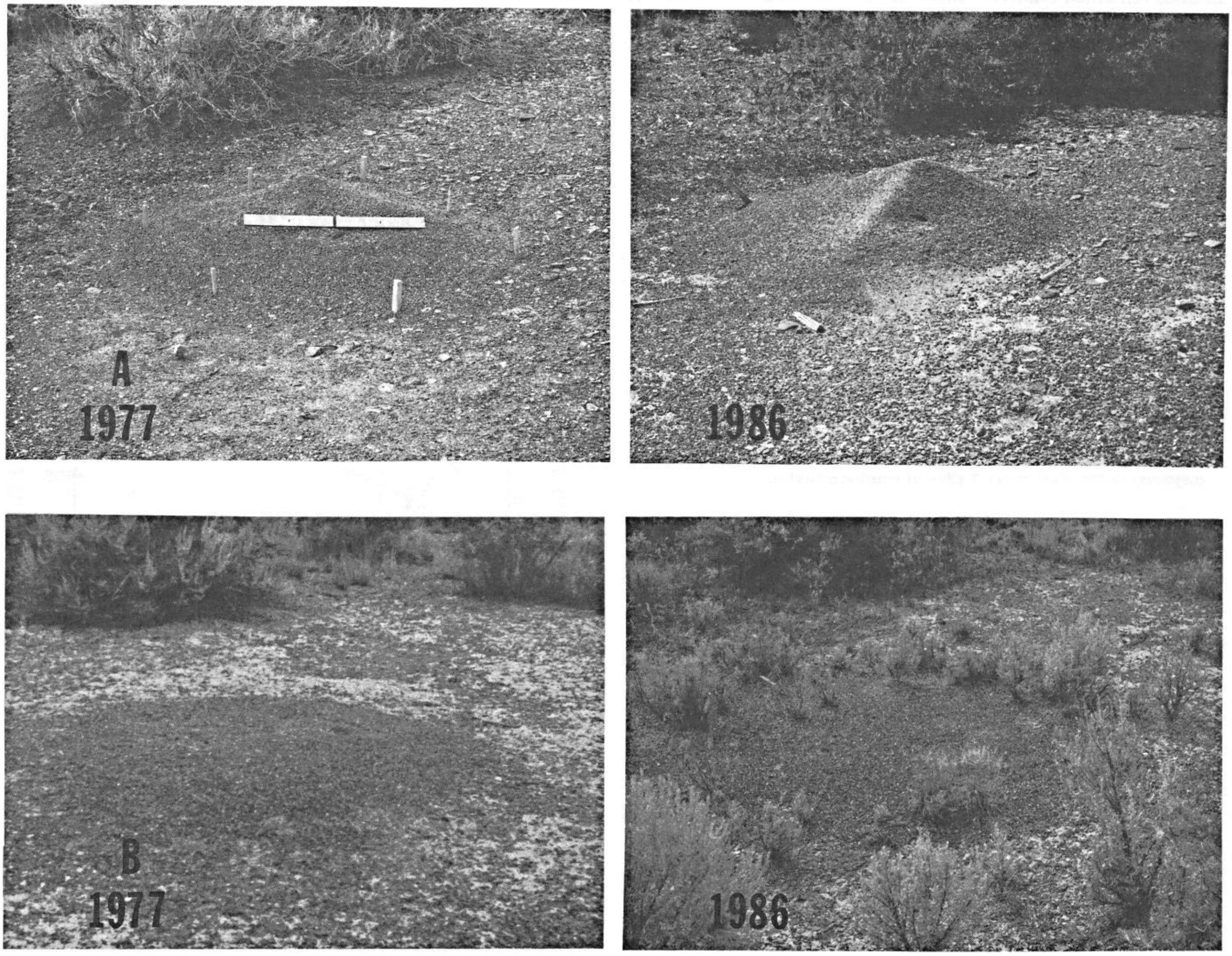

Fig. 3. *(A) An active harvester ant mound* (Pogonomyrmex owyheei) *in 1977 with a 2 ft ruler (62 cm) and the same mound again in 1986. The 1986 photograph was taken a meter or so to the right of the 1977 one. (B) A large active mound in 1977 before it was poisoned and the same mound in 1986 after 9 years of inactivity.*

were badly deteriorated and not more than 2–4 cm in height. Clearings associated with those mounds had also deteriorated, and most had young sagebrush (Fig. 3B) or perennial grasses growing on them.

Discussion

Colony Longevity

Harvester ant colonies are apparently very long lived once they become established. Estimates of longevity ranged from 14 to 30 years with a mean of about 17 years (Table 1). We were not able to determine the age distribution of these colonies, but the fact that substantial mortality occurred in all mound sizes indicates that survivorship is probably closer to a type II curve (mortality independent of age) than a type I curve (old-age mortality). If this is the case, then the age of colonies at death would vary considerably and some would easily reach 25–30 years. Colony longevity has been reported for a number of other ants, but most of these reports are fragmentary or based on single laboratory colonies. Colonies with multiple queens are potentially immortal because new queens are recruited as old ones die (Wilson 1971). Colonies with a single queen may live 5–30 years (Baroni-Urbani et al. 1978, Chew 1987, Tschinkel 1987, Weber 1972), but most species probably do not survive nearly as long in the field due to the rigors of competition, predation, pathogens, and habitat change.

Of the original mounds in our study, almost 75% (91/122) were still active 9 years later—excluding 6 which were known to have died and then been reactivated. This activity rate was almost 30% higher than would have been predicted assuming a 17-year longevity and a type II survivorship curve. Several possibilities may account for this discrepancy. The most likely one is that some active mounds probably died and then were recolonized during the 5-year period (1981–85) when data were not collected. Also, the age distribution may not have been stable or 17 years may be an underestimate of actual longevity.

Another possibility which could confuse the results would be if mature queens were replaced by young queens after they died; fortunately, this does not appear to be the case. *Pogonomyrmex* colonies are uniformly single-queened (Lavigne 1969, MacKay 1981, unpublished data) and hostile to foreign queens (Hölldobler 1976). The possibility of queen replacement was specifically tested with *P. owyheei's* sister species *P. occidentalis* (Cole 1968). We introduced 1-month-old founding queens into 8 mature laboratory colonies which had been deprived of their mother queens first for 1 week and then for 1 month. Workers in these colonies immediately attacked and eventually killed the introduced queens. In short, these colonies did not replace their mother queen when she died; consequently, colony longevity should be the same as queen longevity.

A colony longevity of 17 years indicates that founding queens have a very poor chance of success. Mature harvester ant colonies produce about 100–300 reproductive queens every year (Lavigne 1969, Rogers et al. 1972, MacKay 1981). Assuming this is also true of *P. owyheei,* the average queen would produce several thousand reproductive queens over her lifetime. Thus founding queens would have less than one chance in a thousand of successfully founding a colony in a stable population.

Mounds

Inactive harvester ant mounds are often recolonized by new colonies. reactivations accounted for 25% (8/30) of new colonies discovered during this study. This should be considered a minimum estimate because some mounds probably died and were reactivated between samples. Reactivation of old mounds probably occurs because these locations were successful in the past and offer immediate advantages associated with a preconstructed mound and clearing. The fact that mounds are recolonized indicates that some have been used by successive colonies for many decades. Recolonization of mounds may also explain why mound volume is poorly correlated with colony size (Lavigne 1969, unpublished data). The fact that abandoned mounds can be recognized for periods of a decade or more is a testament to how slowly soil crusts turn over in cold deserts.

Not all abandoned mounds are reoccupied, however. In fact, 13 of 18 mounds on the removal plot were still inactive in 1986, although at least 3 had been reactivated. It was also surprising to find that the removal plot had recovered to only 20–30% of its original population, even 7–8 years after the original mounds had been poisoned. Apparently, reinvasion of abandoned mounds and sites may take many years and is not always uniform or dependable.

Clearings

Active clearings on our study plots showed very few changes over the 9 years of our study (Fig. 3A). Workers readily removed annuals and seedling shrubs from around their mounds by gradually clipping the leaves off. Juvenile shrubs (<40 cm) were occasionally attacked, but mature shrubs were rarely attacked unless they were actually growing out of the mound or their branches were lying on the ground near the mound. This leads to the question of how mature shrubs are eliminated from clearings.

One possibility is that mounds are initially situated in naturally occurring gaps so that the shrubs do not need to be removed. This is probably true of small clearings (<3 m); however, larger clearings (5–10 m) are too large to have occurred naturally. A second possibility is that mature shrubs are attacked directly and killed by repeated defoliation. This may occur in other areas, but we observed only one instance where a mature shrub *(Atriplex)* was substantially defoliated. A third possibility is that the clearings were formed after fire or pests killed the surrounding bushes. In this case, a succession of colonies inhabiting the same clearing would simply eliminate all seedling shrubs in their clearing while the surrounding shrubs continued to mature. A fourth possibility is that the clearings are gradually enlarged as mature bushes die. In this case, the clearings could be many decades or even centuries old because sagebrush in cold deserts often lives 50–100 years (Ferguson 1964). The ages of harvester ant clearings probably vary considerably from area to area and vegetation type to vegetation type. It does seem clear, however, that at least some of these clearings are very old.

One interesting aspect of harvester ant clearings is that they increase the heterogeneity of range habitats. For instance, soil texture and algal crusts are often very different in cleared areas. These clearings also tend to accumulate both water and nutrients (Rogers and Lavigne 1974) which results in increased plant growth around the clearing perimeters (Wight and Nichols 1966). It is conceivable that harvester ant clearings may actually benefit some ranges by allowing rings of continued plant growth during droughts; this perimeter effect could also increase species diversity and perhaps even community stability by serving as temporary refugia for arthropods and other small animals.

Conclusion

Harvester ant colonies in southern Idaho appear to be extremely persistent K-selected organisms. The number of colonies in our study plots remained stable over 9 years of observations. Worker ants only live for a year or two (Porter and Jorgensen 1981), but the colonies themselves may live for several decades (Table 1). Queens apparently live as long as the colony, making them among the longest lived of rangeland animals. Harvester ant mounds and clearings can be reoccupied; consequently, some may persist for many decades.

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Some vegetation responses to selected livestock grazing strategies, Edwards Plateau, Texas

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Abstract

Understanding the temporal response of vegetation to selected livestock grazing strategies is necessary for the continued maintenance or increased productivity of rangelands. Vegetation cover and above-ground biomass were sampled bimonthly from 1978–1984 on pastures grazed continuously (MCG) and moderately stocked (8.1 ha AU^{-1}); continuously (HCG) and heavily stocked (4.6 ha AU^{-1}); high-intensity, low-frequency (HILF) and moderately stocked (8–1; 17:119 day stocked at 8.1 ha AU^{-}); short-duration grazing (SDG) and heavily stocked (14–1; 4:50 day, stocked at 4.6 ha AU^{-1}); and livestock exclusion (LEX). Prior grazing history, vegetation cover, soils, and slope were similar among pastures. Midgrass cover was eliminated in the HCG pasture, and declined in the heavily stocked SDG pasture. Midgrass cover was maintained under the moderately stocked HILF grazing strategy and increased under MCG or LEX. During 1984, sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.) basal diameter in the MCG and LEX pastures was significantly greater than in the SDG pasture. By the end of the study, total organic cover and total aboveground biomass in the MCG or LEX pastures were significantly greater than in the SDG and HCG pastures. The heavy grazing intensity used in this study, regardless of the grazing strategy, does not appear suited for long-term maintenance of midgrass species.

Key Words: vegetation cover, aboveground biomass, bunchgrass, sodgrass

Rangeland vegetation is presumed to have co-evolved with grazing animals, and as a result most rangeland vegetation possesses some level of grazing tolerance (Mack and Thompson 1982). The magnitude of impact that livestock grazing may have on a plant community is therefore dependent upon intensity of grazing. Grazing schemes can be divided into 2 broad categories: (1) continuous year-long or season-long grazing; and (2) periodic grazing. Grazing systems are included in the latter because they are defined as systematically recurring periods of grazing and deferment for 2 or more pastures or management units (Kothmann 1974).

Vegetation composition is used as an indicator of range condition. Ellison (1960) concluded that successional trends in plant communities are proportional to grazing intensity, with most severe changes occurring under heavy grazing. Heavy grazing pressure tends to damage the most palatable species and reduce their abundance (Dyksterhuis 1949, Cottam and Evans 1945). Loss of preferred species is usually associated with a decline in the nutritional value of the available forage and a decline in available forage (Boudet 1975). Compositional shifts in perennial plants are especially important indicators of range condition because their decline is usually associated with increased erosion hazard (Walker 1974). It has been shown generally that as grazing intensity increases, vegetation composition shifts from a midgrass to shortgrass dominance (Rhoades et al. 1964, Sharp et al. 1964, Wood and Blackburn 1984). These shifts in composition have been shown generally to result in a reduction in water infiltration rates and accelerated soil erosion which, ultimately reduces the long-term productivity of rangelands (Thurow 1985; McCalla et al. 1984a, 1984b; Blackburn 1984). The objective of this study was to assess the temporal response of some vegetation variables to selected livestock grazing strategies.

Materials and Methods

Study Area and Treatments

Research was conducted at the Texas Agricultural Experiment Station, which is located in Edwards and Sutton counties (31° N; 100° W) approximately 56 km south of Sonora, at an elevation of 632 m. The mean frost-free period is 240 days. Annual precipitation at the station is highly variable in amount (annual median precipitation, 1918–1984 = 438 mm; range = 156 to 1,054 mm) and events vary seasonally. Cool-season precipitation (October–April) is generally the result of frontal storms characterized by slow, steady rainfall. During the warm season (May–September), most precipitation events are brief, intense convective storms. During this study (1978–1984), an average of 13 storms (range 6–17) with rainfall of 5 mm or more per storm occurred during the 7 warm seasons. These storms accounted for 92% (range 87% to 95%) of the warm-season rainfall. In general, March–July 1978 and April–August 1980 were periods of drought and September 1980 through August 1982 was a period of well-distributed, greater than median precipitation (Fig. 1). In 1978 only 24 mm of rain fell from February 18 to May 19 and no rain fell during the periods of June 8 to July 27 and August 8 to August 28. In 1980 only 6 mm of rain fell from June 11 to August 8. The stress on plants was further intensified during this period by 49 consecutive days with maximum temperatures of 35° C or greater.

During January 1978, three 6-ha study pastures were established by subdividing a larger pasture that had been stocked at a moderate continuous rate of about 8.1 ha AU^{-1} since 1949. Treatments established were: (1) a continuously grazed (MCG) strategy moderately stocked at 8.1 ha AU^{-1}; (2) a continuously grazed (HCG) strategy heavily stocked at 4.6 ha AU^{-1}; and (3) a high- intensity, low-frequency (HILF) pasture used to simulate an 8 pasture rotation grazing strategy (8–1; 17:119 day) moderately stocked at 8.1 ha AU^{-1}. During January 1980, the HILF strategy pasture was changed to a short duration grazing strategy (SDG) (14–1; 4:50 day) and stocked heavily at 4.6 ha AU^{-1}. Even though the stocking rates were similar in the HCG and SDG pastures, grazing pressure index was greater in the SDG pasture. An animal unit ratio of 50% cattle, 25% sheep, and 25% goats was used on the HILF/SDG and HCG pastures. Due to the small pasture size, the 50:25:25 grazing ratio could not be precisely maintained in the MCG pasture. Sheep and goats were grazed continuously with a cow grazed intermittently to maintain the moderate stocking rate.

In January 1980, a 3 ha livestock exclosure (LEX) was established adjacent to the 3 grazing treatment pastures. This site shared

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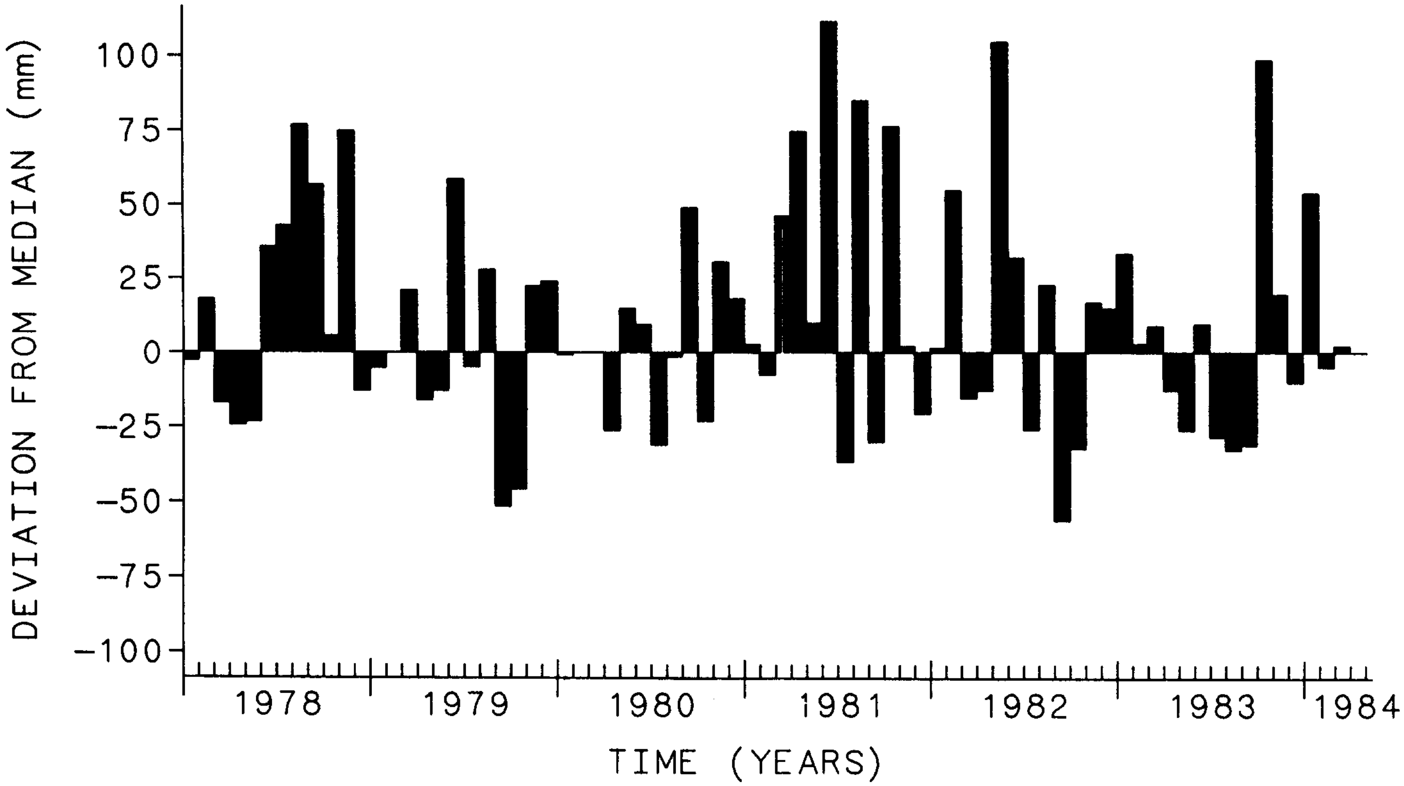

Fig. 1. *Deviation from monthly median precipitation during the study period on the Edwards Plateau, Texas. The monthly precipitation median is based on the 67-period of 1981-1984.*

the same grazing history of the MCG, HCG, and HILF/SDG pastures prior to 1978. However, in 1978 and 1979, the LEX site was grazed at a rate of about 6 ha AU^{-1}. Consequently, vegetation trend in the LEX pasture in 1980 was down compared to when the MCG, HCG, and HILF/SDG pastures were established in 1978. The LEX pasture was located on a site with a clayey loam soil that had a higher sand content and greater slope than the other 3 pastures.

Soils in the study pastures were Tarrant silty clays and soil depth overlaying a fracture limestone substrate ranged from about 150 to 450 mm. Textures of this clayey-skeletal, montmorillonitic, thermic family of Lithic Haplustalls ranged from silty clay loam to clay. There was no consistent mean textural difference between the soils of the SDG/HILF, MCG, and HCG pastures. The surface soils of the LEX pasture had lower clay and higher sand content than the other 3 pastures. There was no detectable change in soil texture in any pasture during the study period.

The vegetation in the pastures is characterized as an oak-grassland community (Smeins et al. 1976, Huston et al. 1981). Woody plant distribution was clustered with the dominant species being live oak (*Quercus virginiana* Mill.). The most common midgrasses were sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.), and threeawn (*Aristida* spp.). Dominant shortgrasses were curlymesquite *(Hilaria belangeri* (Steud.) Nash) and hairy grama (*Bouteloua hirsuta* Lag.).

Methods

Basal and aerial cover characteristics, herbaceous standing crops, and mulch accumulation were estimated bimonthly in the grazed pastures from March 1978 through 1984, and every 4 months from May 1980 to March 1984 in the LEX pasture. Sample locations were randomly assigned to gridded areas within each pasture prior to initiating the grazing strategies. During each sample period, ten 0.45-m^2 plots were randomly assigned to midgrass and shortgrass strata within the gridded area. This sampling procedure prevented the destructive sampling of any site more than once during the study. Areas adjacent to fences and watering locations were excluded to avoid differential livestock use patterns associated with these structures. Due to scarcity of midgrass plants in the HCG pasture, sampling of those plants was discontinued after May 1980. For each plot the percent foliar cover of midgrass, shortgrass, forbs, litter, rock (>5 mm), and bare ground was determined by ocular estimate using a 4-cm gridded frame. Standing crop of grasses and forbs was harvested by clipping. Mulch accumulation was harvested by hand following clipping. All organic material was dried at 60° C prior to weighing.

Surface roughness of each plot was measured with a relief meter (a frame with a set of 10 pins placed 60 mm apart) (Kincaid and Williams 1966). A representative surface roughness index was obtained by measuring the relief of 3 different lines across each plot and then calculating the standard deviation of the pin height.

In addition to the destructive sampling technique described above, 9 permanent 0.25-m^2 vegetation plots were established in each pasture during August 1980. A 10-point frame (Brown 1954) was used bimonthly to measure canopy and basal cover on these plots. A total of 250 canopy points and 250 basal points were recorded for each pasture. Vegetation cover was also estimated on a pasture-wide basis using the step-point method. Five hundred points in each pasture were sampled once each August from 1978 through 1984. In September 1984, basal diameter and standing biomass estimates were made in each pasture from 50 randomly chosen sideoats grama bunches, and area clump diameter was made of 50 randomly chosen sacahuista (*Nolina texana* S. Wats.) bunches. Meteorological data were collected at a permanent station located 1 km from the study pastures.

Analyses

Data normality was tested for skewness and kurtosis (Snedecor and Cochran 1971). Because values for surface roughness were

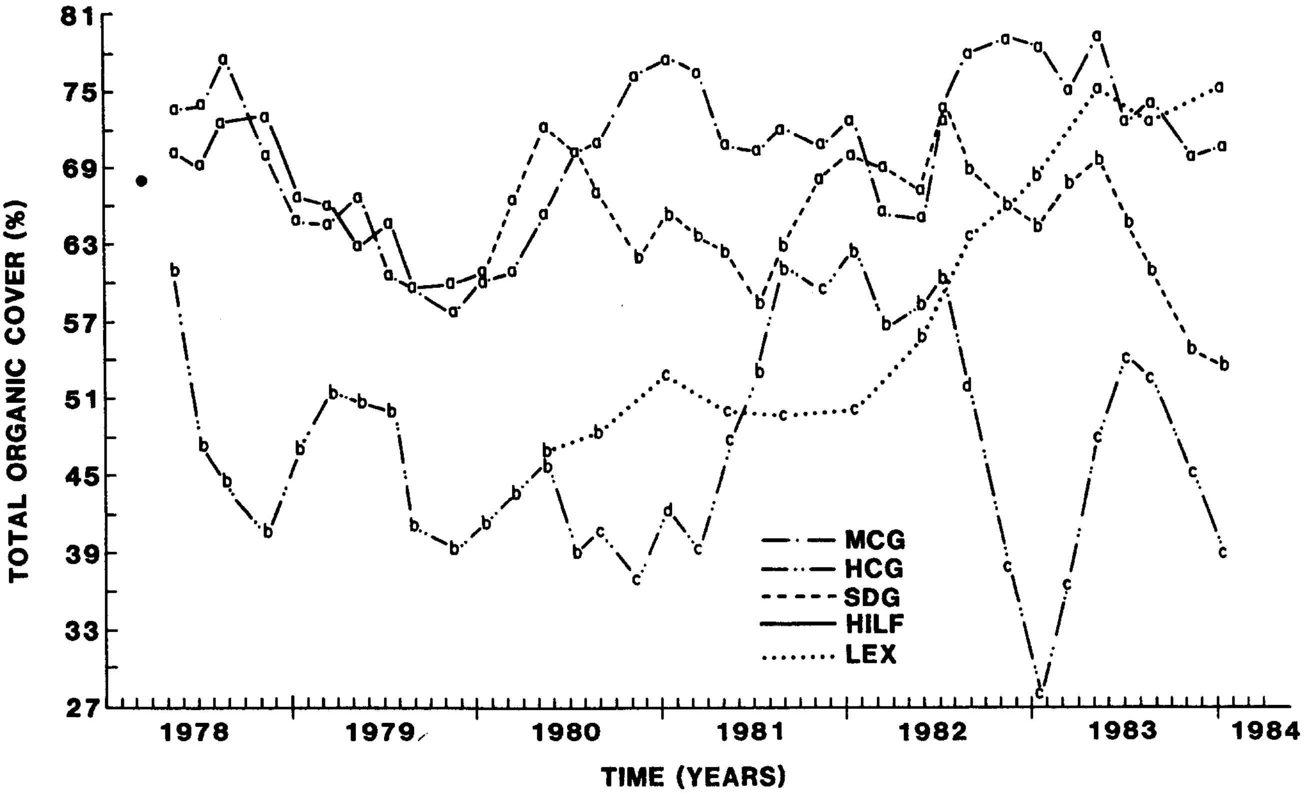

Fig. 2. *Total organic cover (%) as estimated on the 0.45 m^2 plots, Edwards Plateau, Texas. Grazing treatment means with the same letter for the same sample date are not significantly different ($p<0.05$). The dot indicates the composite sample value for March 1978.*

highly skewed, they were transformed using Log_{10} before analyses. Differences among vegetation communities and grazing strategy were tested by analysis of variance. Grazing strategies were not replicated and the error term in the analysis of variance consisted of the nested variation of the randomized sites within the grazing strategies (Dunn and Clark 1974). Treatment means were separated by Duncan's new multiple-range test (Duncan 1955). Correlation analysis (Draper and Smith 1981) was used to assess magnitude of linear association among variables.

Figures 2, 3, 4 and 6 display running averages of 3 sample dates. This procedure aided in graphic display of long-term trends by smoothing variation of individual sample dates that might have resulted from natural site diversity. Data were graphed as weighted composite of the midgrass-and shortgrass-dominated plots. The composite was formed by weighting the percentage of midgrass- and shortgrass-dominated areas in each pasture using the data from the pasture-wide step-point transects. The percentage of midgrass- and shortgrass-dominated areas was updated by treatment on a March to March basis.

Results

Vegetation Cover

Warm-season grasses dominated the study area; therefore, cover began to increase with the onset of the spring growing season. Total organic cover (percent ground cover provided by living and dead organic matter) (Fig. 2) generally continued to increase until mid-summer after which declining soil moisture presumably began to limit growth. The same general pattern was observed for organic basal cover (Thurow 1985). Total organic cover was significantly greater on midgrass-dominated sites (mean total organic cover of 72%) compared to shortgrass sites (mean total organic cover of 59%). Total organic cover of the MCG pasture was less variable than the other grazing strategies during the study. This contrasts with the rapid decline in total organic cover after the HCG strategy was established. Total organic cover of the SDG pasture declined significantly relative to the MCG pasture during the 1980 drought. This difference was maintained throughout most of the remaining 3 years of data collection except during the unusually moist spring of 1982, which prompted rapid forb and shortgrass growth. Total organic cover of the LEX pasture generally increased after the exclosure was established.

Forb cover was dominated by opportunistic, cool-season species. The greatest peaks of forb cover occurred during the cool season following the 1978 and 1980 drought (Fig. 3). In both cases the combined effects of livestock grazing and drought had increased the percentage of bare ground. Bitterweed (*Hymenoxys odorata* D.C.) was the primary species to revegetate the bare areas in the cool season following droughts.

The patterns of midgrass foliar cover and relative dominance were comparable under the MCG and HILF strategies (Figs. 4 & 5). Midgrass foliar cover was essentially eliminated during the first 2.5 years under the HCG strategy. Midgrass foliar cover and relative dominance in the heavily stocked SDG pasture was reduced by approximately one-half from 1980 to 1984 and the trend was definitely downward, even after above-normal rains in 1982. During this same 4-year period, midgrass dominance increased in the LEX pasture. These trends were verified by the statistically similar ($P<0.05$) results obtained on a permanent transect and the step-point transects (Fig. 5). In general, a decline of midgrass relative dominance and an increase in shortgrass dominance was usually associated with heavy livestock grazing and drought. In subsequent years of average or above-average precipitation, midgrass foliar cover increased in the MCG, HILF, and LEX pastures, but vegetation recovery in the SDG and HCG pastures was by shortgrass not midgrass.

Hairy grama and curleymesquite were co-dominant shortgrasses in the LEX pasture, whereas curlymesquite dominated the shortgrass areas in the grazed pastures. Hairy grama, a sod-forming shortgrass, was usually associated with stony-loamy clay soils. The

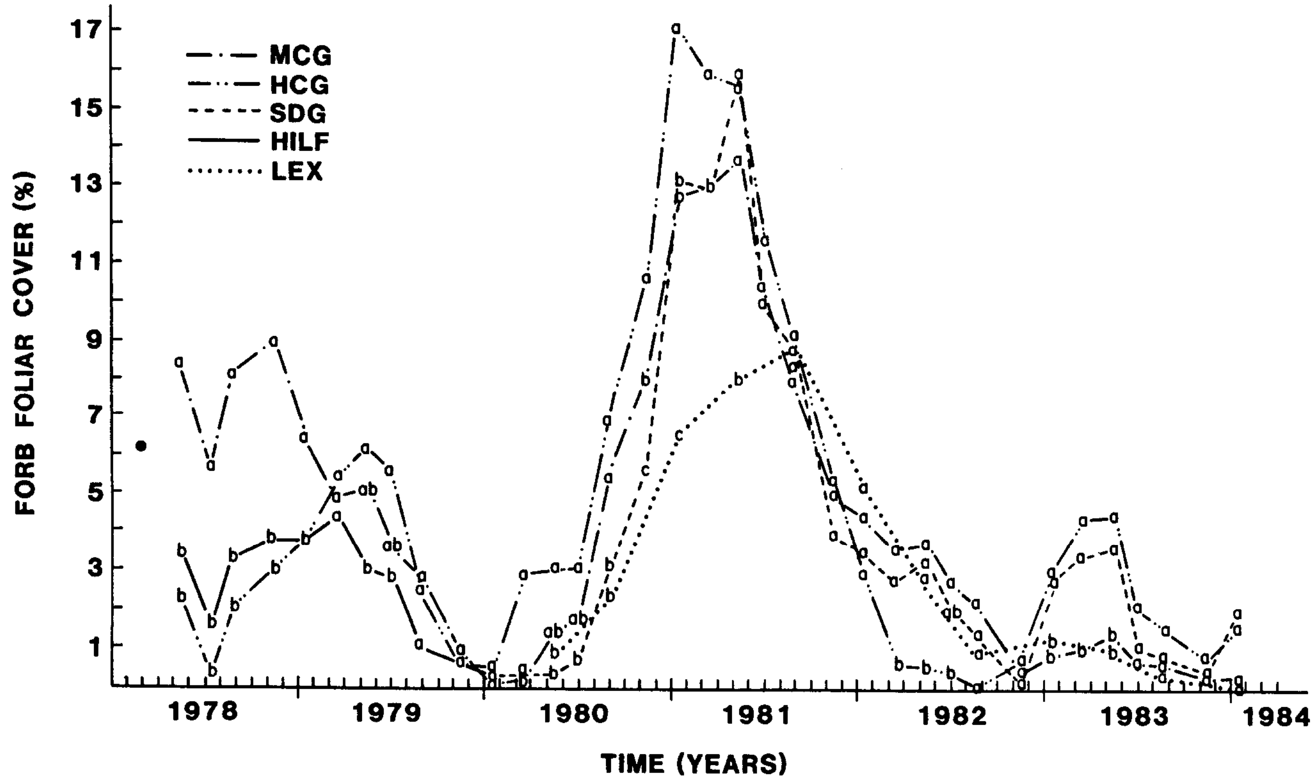

Fig. 3. *Forb foliar cover (%) as estimated on the 0.45-m² plots, Edwards Plateau, Texas. Grazing treatment means with the same letter for the same sample date are not significantly different (p<0.05). The dot indicates the composite sample value for March 1978.*

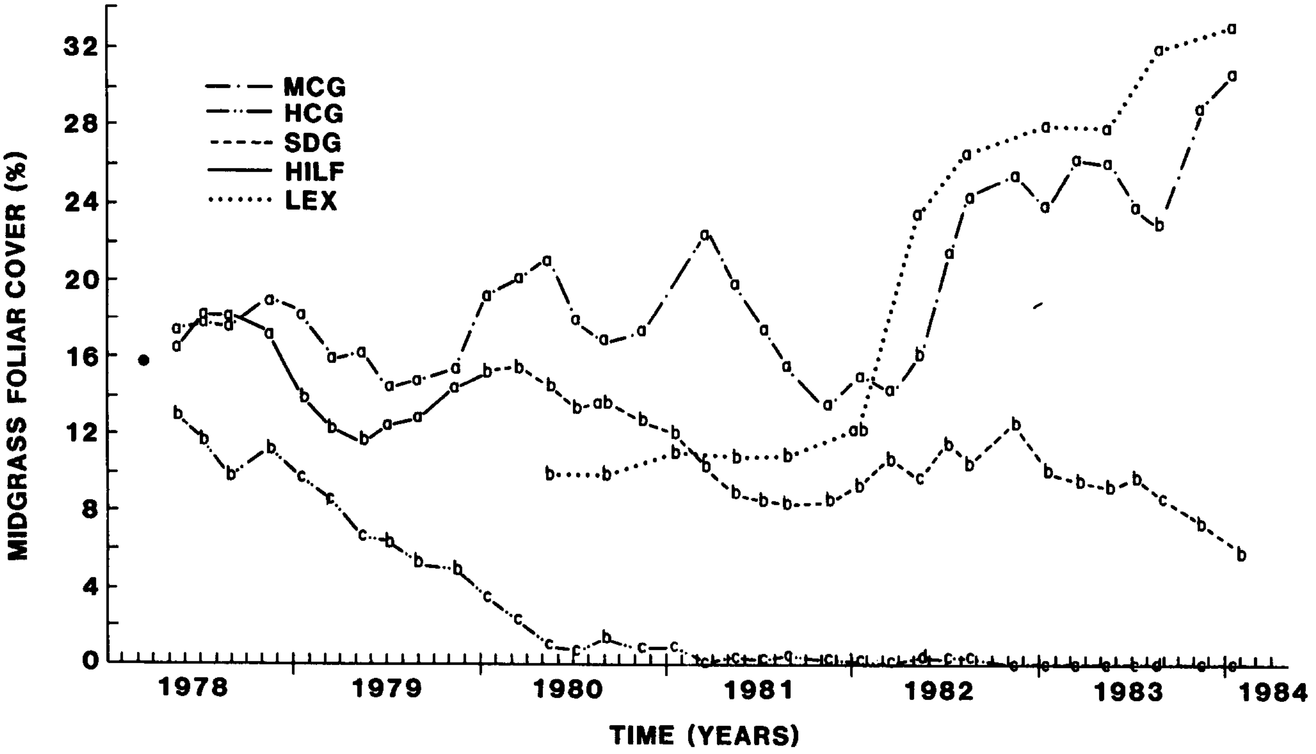

Fig. 4. *Midgrass foliar cover (%) as estimated on the 0.45-m² plots, Edwards Plateau, Texas. Grazing treatment means with the same letter for the same sample date are not significantly different (p<0.05). The dot indicates the composite sample value for March 1978.*

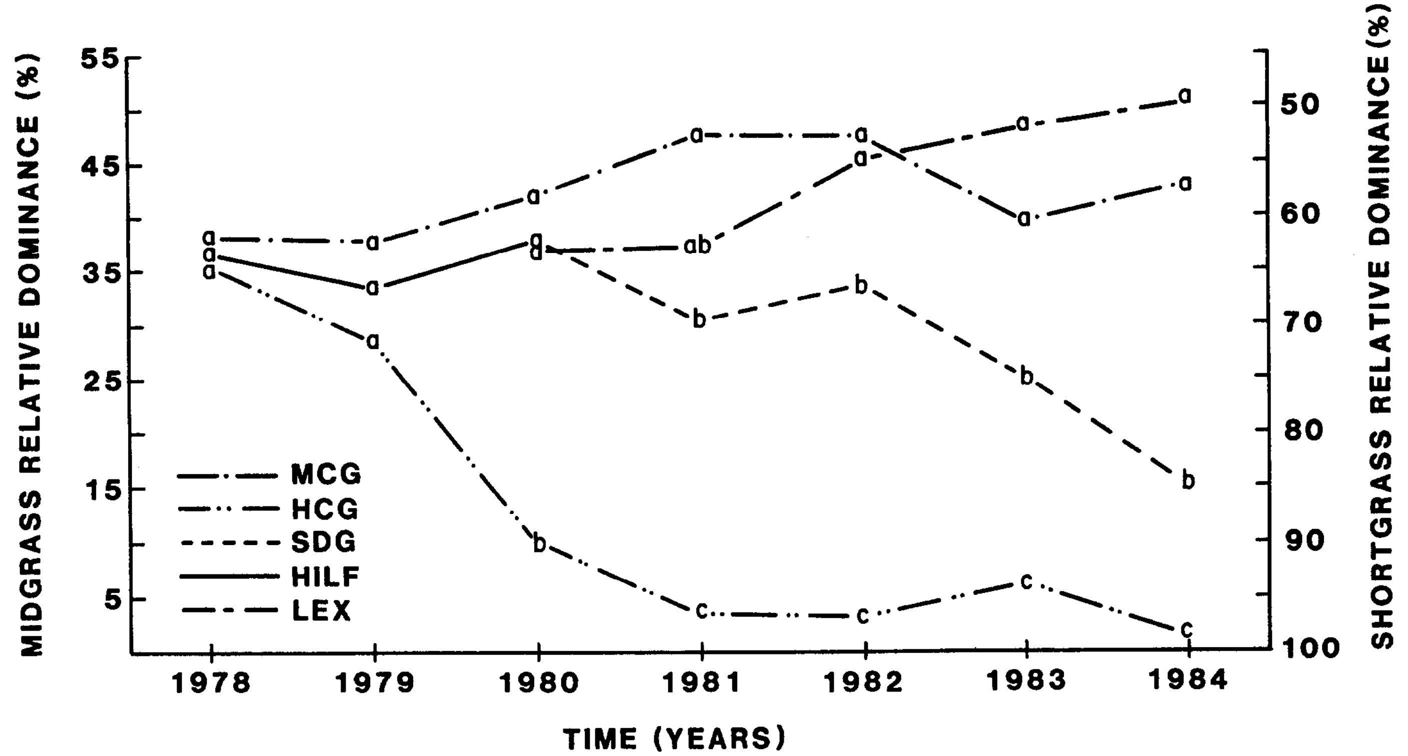

Fig. 5. *Relative dominance of grass life form as estimated by the step-point method on the Edwards Plateau, Texas. Grazing treatment means with the same letter for the same sample date are not significantly different* ($p<0.05$).

stony-loamy clay texture of the LEX pasture was in contrast to the stony-clay soils of the HCG, MCG, and HILF/SDG pastures (Thurow 1985).

Above-ground Biomass and Microrelief

Above-ground biomass declined rapidly under the HCG system and established a new, lower equilibrium that was significantly different from the MCG and HILF pastures (Fig. 6). Above-ground biomass in all pastures declined during the 1978 and 1980 drought. The above-ground biomass of the MCG pasture increased after the 1980 drought and remained significantly greater than that of the SDG and HCG pastures after August 1982. Likewise, above-ground biomass in the LEX pasture steadily increased after the 1980 drought throughout the rest of the study. The above-ground biomass of the SDG pasture was statistically similar to that of the HCG pasture by late 1983.

Basal diameter and standing biomass of sideoats grama bunchgrass clumps were not significantly different in the LEX and MCG pastures, but both were significantly greater than in the SDG pasture (Table 1). Sideoats grama had been eliminated in the HCG pasture. Sacahuista aerial cover diameters were similar in the LEX and MCG pastures, which were both significantly greater than those in SDG and HCG pastures.

The bunchgrass growth form which characterized midgrass cover strongly influenced pasture microrelief (r = .90). However, shortgrass cover was not associated with microrelief (r = .03). Microrelief was consistently greater on midgrass-dominated areas than on shortgrass-dominated areas, primarily because of differences between the bunchgrass and stoloniferous grass growth form.

Discussion and Conclusions

Cover and above-ground biomass declined during the winter dormant season and during drought for all grazing strategies. The nature of those declines and the ability to recover varied between grazing strategy. The HCG and SDG pastures were significantly different from each other and from the MCG and LEX pastures in species composition, basal cover (Thurow 1985), and total organic cover by August 1982. Total organic cover remained fairly constant under the MCG and HILF pastures. The higher stocking rate of the HCG pasture (1.75 times the MCG) caused a sharp decline in total organic cover which coincided with the 1978 drought. The SDG pasture had significantly lower organic cover than the MCG pasture during periods of lower than normal precipitation. The LEX pasture cover did not increase during the favorable precipitation year of 1981. However, a rapid increase in cover began during 1982.

Table 1. Characterization of sideoats grama and sacahuista bunches in the continuously grazed moderately stocked (MCG), continuously grazed heavily stocked (HCG), short duration grazed (SDG), and livestock exclosure (LEX) pastures, Edwards Plateau, Texas (September 1984).

	Sideoats grama		Sacahuista
Grazing strategy	Mean basal diameter (m)	Mean dry standing biomass per bunch (g)	Mean aerial clump diameter (m)
LEX	.37 a[1]	23.1 a	5.0 a
MCG	.39 a	24.5 a	5.1 a
SDG	.30 b	16.2 b	2.5 b
HCG	–[2]	–	2.1 b

[1] Means within each column followed by the same letter are not significantly different ($p<0.05$).

[2] No sideoats grama was present after 7 years of the HCG strategy.

The SDG pasture was stocked at 1.75 times the moderate rate to test the claims that such strategies would increase the primary production of rangelands (Savory 1978, 1979), but there was no

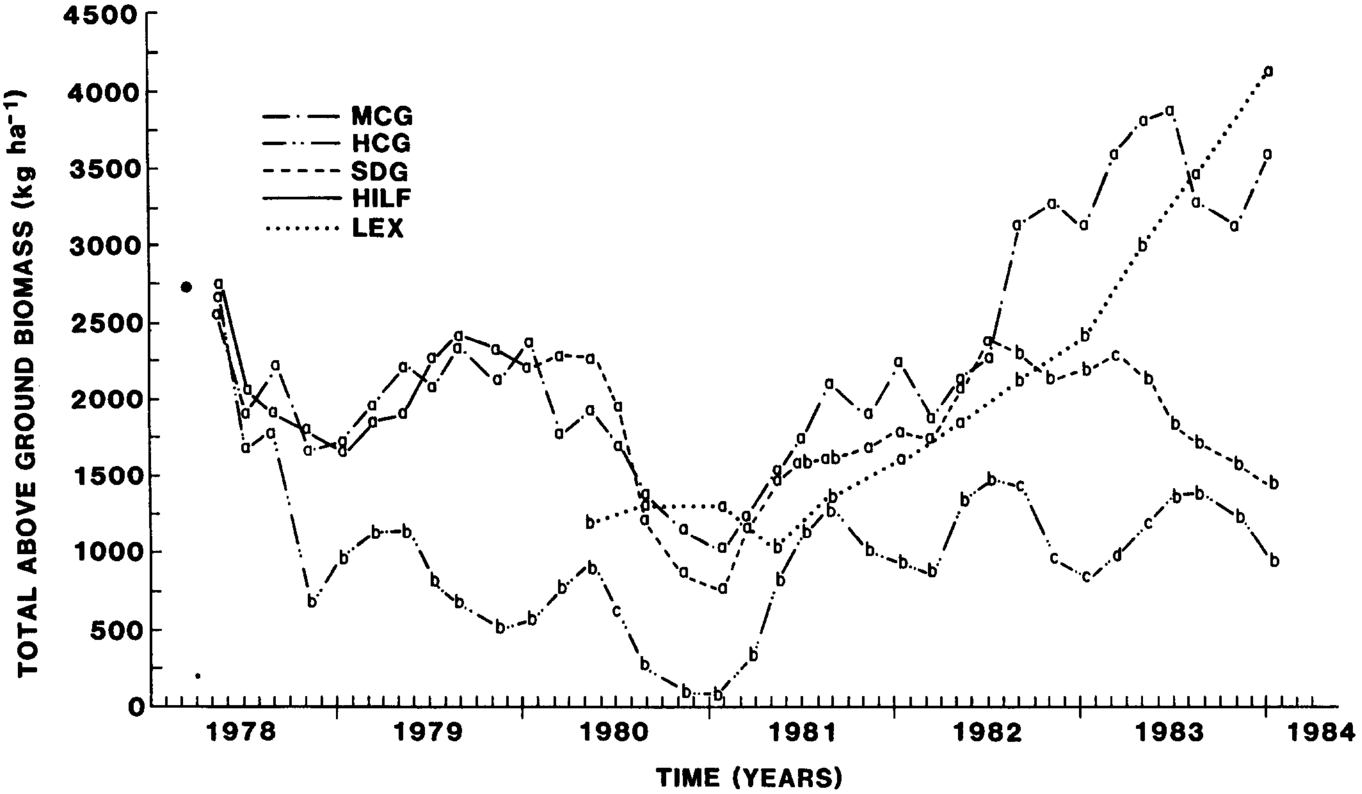

Fig. 6. *Total above-ground biomass (kg ha^{-1}) as estimated on the 0.45-m^2 plots, Edwards Plateau, Texas. Grazing treatment means with the same letter for the sample date are not significantly different ($p<0.05$). The dot indicates the composite sample value for March 1978.*

evidence of increased production with the higher stocking rates (Ralphs 1983). Such a grazing intensity, regardless of the grazing strategy, does not appear suited for long-term maintenance of the desirable midgrass species. The observed vegetation responses in this study were due primarily to drought and excessive defoliation of individual plants caused by heavy stocking rates regardless of the grazing strategy. However, Ralphs (1983) indicated that under the high stocking density of intensive rotation grazing strategies, midgrasses would not maintain themselves even under light stocking rates. There was a clear decline of midgrass cover in both the SDG and HCG pastures during the study (Figs. 4 and 5). In contrast, there was a slight increase in midgrass cover in the MCG pasture and a marked increase in the LEX. The sharp rise of midgrass cover in the LEX pasture that occurred in 1982 was the result of above-average precipitation in both 1981 and 1982 and protection from livestock grazing. General observation indicated a large bunchgrass seed crop in 1981 was followed by establishment of bunchgrass seedlings in 1982. In contrast, the steady decline of midgrass cover in the SDG and HCG pastures reflected the inability of these species to maintain themselves under the heavier grazing pressure. This shift in species composition affected total cover in that the bunch growth form of the midgrass was much more persistent during the dormant season compared with stoloniferous shortgrass cover, which quickly deteriorated when dormant. This trait of shortgrass cover to rapidly decline during periods of dormancy and rapidly increase during warm, moist periods caused cover and above-ground biomass estimates to seasonally fluctuate in pastures when shortgrass was dominant (e.g., SDG and HCG). Midgrass cover fluctuated relatively little between seasons; therefore, pastures with a well-maintained midgrass component did not show major seasonal fluctuations in total organic cover, biomass, or microrelief. The microrelief caused by bunchgrasses serves as barriers to surface runoff and sediment transport by causing surface runoff to move in a slower, more torturous path. Thus the obstructions provided by the bunch growth form are an important determinant of surface runoff and erosion (Thurow et al. 1986).

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Mule deer-induced mortality of mountain big sagebrush

E. DURANT MCARTHUR, A. CLYDE BLAUER, AND STEWART C. SANDERSON

Abstract

A fence line contrast was provided by a deer fence that bisected a mountain big sagebrush *(Artemisia tridentata* ssp. *vaseyana)* community. The sagebrush community was located on an exposed, west-facing slope that was generally swept free of snow during the severe winters of 1982–83 and 1983–84. On the freeway side of the fence, the site was essentially free of browsing animals, while above the fence, the shrubs were exposed to concentrations of mule deer *(Odocoileus hemionus)*. Considerable big sagebrush mortality was evident after the 2 successive winters of heavy snowfall. Big sagebrush mortality and partial dieback of portions of the canopy were significantly ($P<0.05$) higher in the portion of the community exposed to browsing. Herbaceous species composition also differed between the protected and browsed areas with a higher portion of annual species found in the browsed community. A large number of big sagebrush seedlings germinated in 1984, but failed to establish by 1986. Excessive use of native plants by native large herbivores can have lasting effects on plant communities.

Key Words: *Artemisia tridentata* ssp. *vaseyana*, annuals, cheatgrass, *Bromus tectorum*, browsing, succession, *Odocoileus hemionus*

Big sagebrush *(Artemisia tridentata)*, mountain big sagebrush *(A.t.* ssp. *vaseyana)* in particular, is important winter forage for wildlife and livestock (Welch and McArthur 1986, Personius et al. 1987, Welch et al. 1987). Defoliation (Allred 1941, Hsiao 1986), artificial clipping (Cook and Child 1971), and heavy browsing (Smith 1949) have all been shown to cause loss of vigor and mortality in sagebrush taxa of the subgenus *Tridentatae*. Several researchers have suggested heavy fall, winter, and early spring grazing as a means to reduce sagebrush and favor perennial grass for livestock grazing (Frischknecht and Harris 1973, Laycock 1979). Destruction of sagebrush and other perennials leads to vegetative type conversion in the direction of nonproductive exotic annuals (Pickford 1932, Cottam and Evans 1945, Young et al. 1979, Brotherson and Brotherson 1981, Mack 1981). In the summer of 1984, we observed sizable areas of apparent sagebrush mortality on west-facing, exposed slopes after 2 winters of heavy snow accumulation. The area we sampled is divided by a deer-proof highway right-of-way fence that provided a dramatic visual contrast of sagebrush vigor. The deer-proof fence was constructed in 1972 (personal communication, Utah Department of Transportation). This investigation documents the early successional dynamics of the plant community near Santaquin, Utah.

Materials and Methods

Study Site

The study site (Fig. 1) is adjacent to the I-15 freeway just south of the Utah-Juab County line (R.1 East, T.10 South, S.22 extending into S.23). The natural plant community is a mountain big sagebrush-bluebunch wheatgrass *(Agropyron spicatum)* - Sandberg bluegrass *(Poa secunda)* habitat type that has been degraded so that it includes a large quantity of annuals and biennials (Table 1). The sagebrush was determined to be mountain big sagebrush on morphological (McArthur 1983) and ultraviolet water soluble coumarin compound florescence characteristics (McArthur et al. 1981). Elevation ranges from 1,570 to 1,600 m along the right-of-way fence where the study transects were located to 1,680 m at the crest of the eastern ridge. The area is an undulating but west-facing slope with a general slope of 20 to 30%. The impacted area to the east of the right-of-way fence is 21 ha. The comparable area within the highway right-of-way is 1 ha. Domestic livestock have not used the area for several years.

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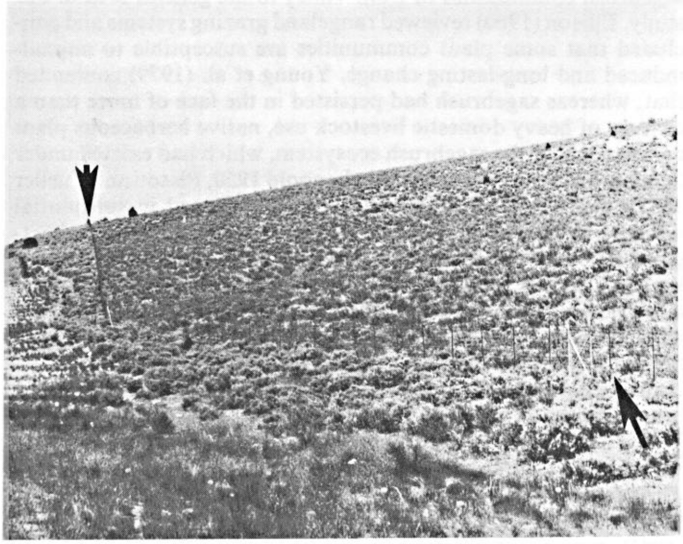

Fig. 1. *Photograph of study site along I-15, south of Santaquin, Utah. Note vigorous mountain big sagebrush below fence (arrows) but less vigorous and dead sagebrush above it.*

Table 1. Species list from study site.[1]

Species	Origin[2]	Longe-vity[3]	Frequency	
			Browsed	Unbrowsed
			--- % ---	
Grasses				
Agropyron cristatum	A	P	0	5.0
Agropyron spicatum	I	P	10.0	32.5
Bromus tectorum	A	A	100.0	100.0
Bromus commutatus	A	P	37.5	2.5
Poa bulbosa	A	P	0	0[4]
Poa secunda	I	P	30.0	22.5
Forbs				
Allyssum alyssoides	A	A	97.5	85.0
Arabis pulchra	I	P	2.5	20.0
Arenaria sp.	I	P	0	12.5
Artemisia ludoviciana	I	P	0	0[4]
Astragalus utahensis	I	P	0	5.0
Cardaria draba	A	P	0	2.5
Epilobium paniculatum	I	A	87.5	50.0
Erigeron divergens	I	B	72.5	57.5
Erigeron sp.	I	A	17.5	0
Eriogonum sp.	I	A	2.5	12.5
Erodium cicutarium	A	A	2.5	0
Helianthus annuus	I	A	62.5	32.5
Lactuca serriola	A	B	92.5	30.0
Leucelene ericioides	I	P	2.5	0
Melilotus alba	A	B	5.0	2.5
Melilotus officinalis	A	B	0[4]	0
Polygonum douglasii	I	A	2.5	0
Ranuclus testiculatus	A	A	37.5	2.5
Streptanthus cordatus	I	P	0	0[4]
Tragopogon dubius	A	B	37.5	15.0
Woody Plants				
Artemisia tridentata ssp. *vaseyana*	I	P	75.0[5]	80.0
Cowania stansburiana	I	P	2.5	0[4]
Gutierrezia sarothrae	I	P	0[4]	0
Juniperus osteosperma	I	P	0	0[4]

[1] After Welsh et al. 1981, 1987 except *Artemisia tridentata* ssp. *vaseyana* and *Cowania stansburiana* for which see McArthur et al. 1981, 1983.
[2] A = adventive, I = indigenous.
[3] A = annual, B = biennial (some may be annual, too), P = perennial.
[4] Present on transect but not in quadrats.
[5] Does not include standing dead.

Methods

Four paired, 50-m transects were located randomly along the 600 m length of the right-of-way fence in and opposite the impacted area. None of the transects overlapped linearly. None of the transects appeared to have been physically disturbed by the highway or fence construction. Frequency and density of each species (number of individual plants, including seedlings) was collected on m^2 quadrats every 5 m along transects (10 per transect). Data from individual mountain big sagebrush plants were collected from the mature plant nearest each 5-m transect mark. Height, total crown diameter, and live crown diameter were recorded in centimeters, and vigor and use were recorded on a numerical rating scale. Vigor scale was 0 = dead to 4 = vigorous. The use scale was 1 = no use observed to 4 = very heavy use with most leaves gone, annual twig growth consumed. Deer pellet group data were collected along each transect in a 2-m wide band (2 by 50 m). Data were collected during the first week of August 1984. The number of sagebrush seedlings per quadrat was collected again on 10 July 1986. Seedlings were defined as any young plant less than 10 cm tall.

Data were analyzed using t-tests, Mann-Whitney U tests, χ^2 analysis, and one-way analysis of variance (Pollard 1977). Percentage data were arcsine transformed before analysis but changed back to percentage for presentation.

Results and Discussion

Sagebrush Plants

There was a significant ($P<0.5$) mortality and decline in vigor of mountain big sagebrush plants in the area behind the right-of-way fence where mule deer *(Odocoileus hemionus)* had access (Table 2).

Table 2. Some comparisons of plant densities between browsed and nonbrowsed transects, 1984.[1]

Plant group	Browsed	Non-browsed	t or U[2]	P[3]
Annual grasses	96.2	66.6	1.42	.17
Annual forbs	73.3	42.2	2.90	.03*
Total annuals	169.5	108.8	4.52	.01*
Perennial grasses	0.7	1.4	1.23	.15
Perennial forbs	0.3	1.0	1.36	.14
Total perennials[4]	1.0	2.4	1.67	.10
Sagebrush plants[5]	1.8	1.9	0.85	.45
Live sagebrush plants[5]	1.2	1.8	3.51	.02*
Sagebrush vigor[6]	1.4	2.6	16	.05*
Sagebrush use[6]	3.3	1.2	16	.05*
Deer pellet groups	0.5	0.01	5.34	.01**

[1] Data, except scaled ratings[6], presented on a number per square meter basis; n = in all cases.
[2] Paired t-tests except for scaled ratings for which a Mann-Whitney U test was used (see Methods section).
[3] * = $P\leq0.05$, ** = $P\leq0.01$.
[4] Excludes woody plants.
[5] Sagebrush plants category includes standing dead plants. The live sagebrush plants browsed on transects were reduced in vigor as well.
[6] These data were based on rating scales: Vigor: 0 = dead...4 = vigorous. Use: 1 = no use...4 = heavy use (see Methods section).

Mule deer forage access was limited to the exposed slopes with less snow accumulation in the area during much of the 1982–1983 and 1983–1984 winters. These winters had heavy snow accumulation. From 1 November to 31 March for those winters, 317 and 326 mm of precipitation, most of it snow, fell at the Santaquin weather station, which is located about 3 km away at a comparable elevation (1,561 m) (NOAA 1982, 1983, 1984). That is 141 and 148% of normal precipitation (225 mm) for ther period (Stevens et al. 1983). The heavy concentration of mule deer is demonstrated by the highly significant differences of pellet groups and of sagebrush use on the browsed transect data as opposed to the nonbrowsed transects (Table 2). Mountain big sagebrush plants were quite similar in height and crown diameter on both sides of the right-of-way fence ($\bar{x} = 56.7$ cm tall on browsed side versus 69.4 on the nonbrowsed side; $\bar{x} = 84.9$ cm crown diameter on the browsed side versus 93.2 on the nonbrowsed side), but the number of dead plants was significantly different ($P<0.05$) between the 2 sides of the fence (Table 2). Live crown diameter was also different (by analysis of variance: DF = 1, F = 30.6, $P<0.01$): plants in the browsed transects had an average crown dieback of 64% in comparison to a 17% dieback in the nonbrowsed transects. Dead plants were 11 times as common on the browsed side of the fence. However, in areas of low relief on the browsed side of the fence, where mountain big sagebrush plants were afforded protection by deep snow cover, sagebrush plants were healthy.

Our results support published reports that sagebrush does not tolerate heavy defoliation. Cook and Child (1971) demonstrated that simulated browsing (clipping) twice (winter and spring) killed all big sagebrush plants and all but about 3% of black sagebrush plants *(Artemisia nova)*. Single clipping events were also damaging to big and black sagebrush plants; late spring was almost as damaging as the double event, but winter and early spring were less damaging (Cook and Child 1971). Smith (1949) reported that twice as many big sagebrush plants were dead as alive on a heavily used mule deer winter range, whereas on an adjacent livestock range 6 times as many big sagebrush plants were alive as were dead. Smith did not recognize big sagebrush at the subspecies level, but his study area currently supports mountain big sagebrush. Defoliation of various sagebrush taxa by insects also causes loss of plant vigor and death (Allred 1941, Hsiao 1986, McArthur unpublished). There are other reports in the literature describing mortality of sagebrush induced by browsing, but they are mostly anecdotal. This report, so far as we know, is the first to quantify the effects of heavy mule deer browsing on mountain big sagebrush. Such information is important inasmuch as some populations of mountain big sagebrush are preferred mule deer winter forage (Welch and McArthur 1986, Personius et al. 1987), and sagebrush in general is an important winter food for mule deer and other animals throughout the West (McArthur and Welch 1986).

Vegetative Community Dynamics

The natural plant community of the study site was degraded even prior to heavy browsing brought on by the concentration of mule deer during the winters of 1982–1983 and 1983–1984. This condition is evident by the number of annual grasses and annual and biennial forbs present on the nonbrowsed (highway right-of-way) transects (Table 2). Seeding along the freeway right-of-way on the roadcut did introduce a few plants that subsequently invaded the nonbrowsed transects, crested wheatgrass *(Agropyron cristatum)* and perhaps sweetclover (*Melilotus* spp.) (Table 1). However, prior to construction of the freeway and fence in 1972, the plant community was unified and in all likelihood homogeneous. Some differences may have been emerging by 1982 due to different animal use patterns as a consequence of the construction of the deer-proof fence. We believe, however, that the high snowfall of back-to-back winters (1982–1984) forced deer into an area relatively free of snow because of its sloping western exposure and hence with available forage but bounded by areas of deeper snow and the deer-proof fence. Deer use was unequivocally heavy in the browsed transects. Both sagebrush use and density of deer pellet groups were significantly higher there than on the unbrowsed transects (Table 2). The value of 0.52 pellet groups per m^2 (= 5,200/ha or 2,105/ac) is high. Using a value of 14 pellet groups per day per deer (Smith 1964), our data indicate approximately 370 deer days use per hectare (150 per acre). We do not imply precision with these data because of our relatively small sampling area and the possibility that some of the pellets were not of the current season. Nevertheless, the data indicate heavy deer use.

Young et al. (1979) reviewed the status of the greater sagebrush ecosystem and made a case for an extensive disclimax situation. Brotherson and Brotherson (1981) documented degradation of sagebrush communities in Utah Valley in the general area of our study. Ellison (1960) reviewed rangeland grazing systems and concluded that some plant communities are susceptible to animal-induced and long-lasting change. Young et al. (1979) contended that, whereas sagebrush had persisted in the face of more than a century of heavy domestic livestock use, native herbaceous plant components of the sagebrush ecosystem, which had existed under light herbivore use for millennia (Leopold 1950, Platou and Tueller 1985), had not fared well but had been replaced in substantial measure by short-lived exotics. At our study site these are cheatgrass *(Bromus tectorum)*, alyssum *(Alyssum alyssoides)*, prickly lettuce *(Lactuca serriola)*, yellow salsify *(Tragopogon dubius)* and a few others (Table 1). The recent heavy browsing pressure documented in this study, however, has dramatically shifted the balance further toward the disclimax. Note the overall (Table 2) and particular species (Table 1) increases for the short-lived plants in the browsed area.

Our data represent only one point in time. However, it is easy to visualize that sustained perturbations, whether by browsing animals as demonstrated in this case or by grazing animals as suggested by Pickford (1932), Ellison (1960), and Brotherson and Brotherson (1981), can change vegetative communities for long periods. Fire, another perturbation, can also have dramatic effects. Cheatgrass is a fire and other disturbance climax species that sustains itself by burning and reburning or other disturbance factors, thus eliminating much of the native perennial competition (Piemsiel 1951, Mack 1981).

We wondered if mountain big sagebrush was recovering after 2 open winters (NOAA 1984, 1985, 1986). None of the dead sagebrush had resprouted by 1986. Furthermore, the promising cohort of seedlings on the browsed side of the fence (39.0/m^2) of 1984 was reduced to a very low level in 1986 (0.05/m^2) ($\chi^2 = 176$, DF = 1, $P<0.01$). We suspect the cohort was lost because of competition with the dense stand of annuals and normally very hot and dry mid-summer conditions. August 1985 was even drier than normal (<5 mm vs 28 mm of precipitation) (NOAA 1985). No seedlings were found in any quadrat in 1984 or 1986 on the highway right-of-way side of the fence.

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Our members in other countries are not sitting idle. I have recently heard encouraging reports of progress being made to establish range management courses in several universities in Central and South America.

Another important area is our *affiliation* with other organizations having similar interests and objectives. We can learn from these organizations a well as find strength and effectiveness in numbers. SRM now has 16 affiliate organizations that we maintain contact with through the Affiliations Committee.

One that we are working closely with at the present time is the National Association of Conservation Districts. Along with the Public Lands, Pasture and Range Committee of NACD, we have appointed one member from each organization in several states to coordinate and provide emphasis for Coordinated Resource Management and Planning. That group of people held their first meeting here at Corpus Christi.

What does SRM do? The next time someone asks that question, these are some things you might respond with. I know there are more. Some of you are probably thinking, "Why didn't he mention such and such?" I'm sure you are getting tired of sitting and I don't want to carry this out much longer.

However, I would be remiss if I didn't take time to express appreciation for the help I have received this year.

First of all, I would like to thank Pete Jackson and the headquarters staff, including the Washington, D.C. Liaison. You would have to look a long time to find a more dedicated group. I still marvel at the efficiency with which they made the move into the new office building. Pete keeps going at a high lope that wears me out just to try and keep up.

I also want to thank the Committees and Sections for the hard work over the past year. I see the Sections becoming increasingly active and that makes me feel good. I have often said that active Sections with their own committees and programs of work, that pull in the same direction, increase the effectiveness of SRM many times.

Finally, thank all of you, the members of this fine organization. It has been a pleasure to serve you.

Cattle grazing tall larkspur on Utah mountain rangeland

JAMES A. PFISTER, MICHAEL H. RALPHS, AND GARY D. MANNERS

Abstract

Ingestion of tall larkspur (*Delphinium barbeyi* L. Huth) is a major cause of cattle death on ranges where the plant occurs. The amount and timing of tall larkspur ingestion by grazing cattle was studied from 30 July to 2 September 1986 on high mountain rangeland in central Utah. Forbs dominated the vegetation and were also the major dietary item selected by cattle (>70% of total bites). There was a negative relationship (r=-0.62) between standing crop of other forbs and tall larkspur consumption. Cattle began eating substantial quantities (>10% of bites) of tall larkspur about 10 August, and consumption had increased to 20% when the study ended. Tall larkspur leaves and pods were the major parts selected. At the time of major consumption, leaves were relatively low and declining in total alkaloid concentration (TAC) (1.0–0.6%) while pods were approximately 1.0% TAC and increasing when the study ended. Time spent per feeding station (TFS) was influenced by the vegetation area where animals foraged. TFS in the grass-forb, currant (*Ribes* spp.), and larkspur areas were 11.2, 25.9, and 22.0 s, respectively. Cattle grazed most efficiently (bite rate:step rate) in the grass-forb areas, and least efficiently in the currant areas. Cattle ate large quantities of tall larkspur during the study with no deaths, probably due to the low alkaloid levels in the tall larkspur. Larkspur consumption was not correlated with previous 12- or 24-h precipitation totals. However, cattle did begin major consumption of tall larkspur after 2 rain showers fell following a several week dry period.

Key Words: poisonous plants, alkaloids, larkspur grazing, cattle grazing behavior

Larkspur (*Delphinium* spp.) poisoning is a major cause of livestock losses on mountain ranges (Williams and Cronin 1966). Cronin (1971) reported that tall larkspur was responsible for more cattle *(Bos taurus)* losses in central Utah than all other poisonous plants. Even though cattle typically graze these mountain ranges for short periods of time during the summer, death losses attributed to larkspur poisoning have been severe (2 to 12%, mean 4.3%) for some USDA Forest Service grazing allotments experiencing persistent losses (Cronin et al. 1976). Cattle losses on high (>3,000 m) mountain ranges generally are greatest during the first 2 to 3 weeks of the grazing season (Williams and Cronin 1966, Knowles 1974). Other work indicates a bimodal peak to losses, with some deaths occurring during the latter portion of the grazing season (Cronin et al. 1976).

The toxic components of tall larkspur are alkaloids. Ingestion of toxic quantities of larkspur progressively induces restlessness, stiff movements, then a straddled stance before sudden collapse (Olsen 1978). Death is from respiratory failure. Early studies suggested that toxicity of larkspur plants is related to stage of growth (Marsh et al. 1916). Williams and Cronin (1966) found the plant highest in alkaloid levels during the early stages of growth, with new leaves and stem tips containing high concentrations of alkaloids. Studies with rats indicated that toxicity declines with maturity; however the seeds are high in alkaloids (Olsen 1977). Larkspur toxicity cannot be related directly to total alkaloid levels. Individual alkaloids, or combinations of alkaloids vary in degree of toxicity (Olsen 1984).

Little information exists on the amount and timing of larkspur ingestion by grazing cattle. Feeding trials in pens have shown the quantities of tall larkspur that are fatal to cattle, and have characterized the symptoms of larkspur poisoning (Olsen 1978). However, research into plant/animal relationships under grazing situations is needed so that management strategies to prevent or reduce losses can be formulated and tested (Cronin et al. 1976, Olsen 1984). Thus, the objectives of this study were (1) to determine when cattle consumed larkspur in relation to plant phenology and alkaloid levels of plant parts, (2) to determine if a relationship existed between larkspur consumption and standing crop of other available forages, and (3) to quantify aspects of cattle foraging behavior on larkspur-infested rangelands.

Methods

The field study was conducted at the head of Six Mile Canyon, east of Manti in central Utah at an altitude of about 3,200 m. Two habitat types are found on the study area (Bob Thompson, Range staff officer, USDA Forest Service, personal communication). The first is a *Ribes-Agropyron* dominated site, with open grass-forb areas interspersed with dense mottes of currant (*Ribes* spp.). Important grasses in this type are slender wheatgrass *(Agropyron trachycaulum* (Link) Malte), mountain brome (*Bromus carinatus* Hook. & Arn.), and Lettermans needlegrass (*Stipa lettermannii* Vasey). Dominant forbs in this type are Louisiana sagebrush (*Artemisia ludoviciana* Nutt.), mountain dandelion (*Taraxacum officinale* Weber), plantain (*Plantago tweedyi* Grey), and meadow rue (*Thalictrum fendleri* Engelm.). The second habitat type is found on snowdrift areas and is dominated by dense concentrations of tall larkspur. Besides tall larkspur, vegetation in this type consists of sparser quantities of the same major grasses and forbs as found in the *Ribes-Agropyron* type. At the beginning of the study, tall larkspur plants were in various stages of growth from vegetative in areas of recently melted snow to flowering in areas where lesser amounts of snow had accumulated. Soils in the area were montmorillonitic, clayey-skeletal, Pachic Cryoborolls on benches hosting the tall larkspur-dominated tall forb community. Soils were eroded to very shallow solas deposits among coarse limestone cobbles on the slopes (Dan Larsen, soil scientist, USDA Forest Service, personal communication).

The 4-ha study pasture was enclosed with an electric fence. Sufficient forage was available for 4 yearling Hereford heifers (350 kg body weight) to graze the site from late July to early September, 1986. The heifers had grazed in the area the previous summer as calves with their mothers. A bite count technique was used in conjunction with focal animal sampling (Altman 1974) to determine relative amounts of tall larkspur consumed. Each heifer was observed for two, 10-minute periods during the morning beginning just after daybreak. During the afternoon and evening each heifer was observed for three or four 10-minute periods. Bites were recorded in the following categories: tall larkspur leaf, flowering raceme, pod raceme, and stem, grasses (including grasslike), Louisiana sagebrush, *Lupinus* spp., other forbs, and the shrubs currant and elderberry (*Sambucus racemosa* L.).

Average daily grazing time was determined by fitting a heifer with a vibracorder. Time per feeding station (TFS) was determined every 10 days. A feeding station was defined as the amount

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of time an animal spent grazing at a site without moving both front feet (Ruyle and Dwyer 1985). Each heifer was observed during the morning grazing period until 25 feeding stations were recorded. The process was repeated during the afternoon. Simultaneous measurements were made of the steps taken between feeding stations, and the time spent walking between feeding sites. The vegetation area the animal was grazing in was also noted (e.g., currant, grass-forb, or larkspur areas).

Larkspur plant parts were collected periodically for alkaloid analysis. Clipped samples were oven-dried at 60° C and 48 h. A wet weight was taken at the time of harvest to determine dry matter percentage of larkspur throughout the grazing period. The plant material was ground through a 1-mm screen in a Wiley mill and analyzed for total alkaloid concentration (TAC). TAC was determined using a modification of the procedure of Pelletier et al. (1981). HCl was used after ethanol extraction to acidify the extract, and NaOH was used to basify the aqueous layer after extraction with chloroform.

A stratified random sampling scheme was used to determine standing crop. The study area was mapped into 3 discrete plant communities. The *Ribes-Agropyron* type was divided into 2 areas dominated by currant mottes and grass-forbs, respectively. The third plant community consisted of the area dominated by tall larkspur. The grass-forb area was sampled using thirty .25m by 1m-quadrats clipped to 15-mm stubble height at the beginning, midpoint and the end of the trial.

Tall larkspur biomass was determined using a double-sampling procedure. Ten tall larkspur plants were randomly selected along a transect line, the stalks were counted, then a visual weight estimate of each plant was recorded before clipping and weighing. An additional 30 tall larkspur plants were similarly selected, and after counting the number of stalks, a weight estimate was made of each plant. Weights of the 30 estimated plants were corrected with a regression procedure using the first 10 plant weights and estimates. This regression equation was $Y=40.23+1.001X$ ($r^2=.69$, $P=0.0028$), were X is the estimate of larkspur weight and Y is the corrected weight estimate per larkspur plant. Density of larkspur plants on the area was determined using thirty 2m by 4-m plots located along transects in the areas dominated by larkspur. Total larkspur standing crop was then calculated as the weight per plant multipled by the density. This procedure was done only at the beginning of the grazing trial because it became obvious that this procedure was not sensitive to larkspur disappearance over time since cattle grazed only racemes and leaves. No estimation was attempted of the available forage in the very dense currant mottes. There were few other forage species in the dense larkspur areas, thus no additional standing crop measurements were taken.

Utilization of tall larkspur was estimated midway through the study (16 August) and again at the end of the trial (3 September). Forty 1-m^2 plots were randomly located along transects in the larkspur areas. Within each plot, measurements taken included the number of stalks, the number of grazed stalks (apex or leaves removed), and the number of remaining ungrazed flowers or pods (intact apexes).

Rainfall was measured using a precipitation event recorder. Each rainfall event was recorded automatically on a chart which was read daily. Temperature and relative humidity were continuously recorded using a hygrothermograph.

Statistical analysis involved calculating confidence intervals, and *t*-tests where appropriate. Chi-square analysis was used to test for differences in the histograms of TFS and bite rate by vegetation area or date.

Results

Forage available

Forbs were the dominant component of the standing crop (Table 1). Louisiana sagebrush and *Lupinus* spp. were weighed separately due to their relative unpalatability to cattle. There was a significant ($P<0.1$) disappearance of other forbs over time. Graminoids actually increased slightly ($P>0.1$) during the first 2 weeks, then declined ($P>0.1$) during the latter portion of the study. Tall larkspur biomass was 1,330 kg/ha when averaged over the entire study area. However, in the dense patches tall larkspur biomass was nearly 5,000 kg/ha. Larkspur plant parts did not change greatly in moisture content over time. The leaves, flowering racemes, and fruit pods were 75 to 81, 73 to 81, and 78 to 82% water, respectively, during the study period.

Table 1. Standing crop of herbage (kg/ha) on 3 dates on Utah mountain rangeland during 1986.

	Date		
Item	30 July	14 August	3 Sep.
Graminoids	232a	336a	180a
Other forbs	596a	440b	196c
A. ludoviciana	200	184	264
L. alpestris	60	36	48
SUBTOTAL	1088a	996ab	688b
D. barbeyi	1334	–[d]	–[d]

[abc] Means in the same row followed by a common letter have overlapping 90% confidence intervals.

[d] *D. barbeyi* was not measured on these dates; see Table 2 for utilization estimates.

Utilization of Tall Larkspur

Midway through the grazing trial only 15% of the larkspur apexes had been grazed, in contrast to 61% at the end (Table 2). No larkspur stalks with grazed leaves were noted at the mid-point, although cattle had been observed eating a few leaves during the previous week. By the end of the study, over 45% of the stalks had at least 1 grazed leaf. At the midpoint of the trial, most of the ungrazed stalks were in the flower stage (63%) (Table 2), compared to 36% in the pod stage. At the end of the trial, 79% of the ungrazed stalks were in the pod stage. Utilization estimates suggest preference for pods over flowers.

Table 2. Utilization of larkspur (means ± S.D.) by cattle at the midportion (16 Aug) and end (3 Sep) of the grazing period.

	Date	
Item	16 Aug	3 Sep
% grazed larkspur apexes[c]	15.2±20.4a	61.2±25.5b
% stalks with ≥1 grazed leaf	0.0a	45.2±30.7b
% ungrazed apexes with flowers	63.1±31.9a	14.7±12.4b
% ungrazed apexes with pods	35.7±34.6a	79.0±29.4b

[ab] Means in the same row with different letters are different ($P<.05$) as determined by t-test.

[c] Virtually all grazed apexes (flower or pod) were utilized 80–100% (i.e. little residual flower or pod on apex).

Total Alkaloids in Tall Larkspur

Plant parts differed in TAC according to phenological stage of the individual plant on a given date (Table 3). On 1 Aug., leaves from vegetative larkspur plants were highest in TAC (>3.0%), while leaves from plants in full bloom had much lower TAC (1.0%). TAC for stems from vegetative plants were also much higher compared with stem material from flowering plants. Flowers showed an increase in TAC from the bud to full bloom stages of growth. Pods were about 1% TAC near the end of August, and were increasing when the study ended.

Bite Count

The cattle selected little (2.5% of total bites) tall larkspur during early days of the study (Table 4). The proportion of larkspur bites increased as the study progressed until >20% of the bites were

Table 3. Total alkaloid content for tall larkspur plant parts on Utah rangeland during August, 1986.

Plant part	Date	Phenological stage	Total alkaloids[a]
Leaf	1 Aug	vegetative	3.1
Leaf	1 Aug	bud	1.3
Leaf	1 Aug	full bloom	1.0
Leaf	25 Aug	fruit pod	0.6
Stem	1 Aug	vegetative	2.4
Stem	1 Aug	bud	0.6
Stem	1 Aug	full bloom	0.3
Stem	25 Aug	fruit pod	0.4
Flower	1 Aug	bud	0.6
Flower	1 Aug	full bloom	0.9
Flower apex[b]	15 Aug	full bloom	0.6c
Pod apex[b]	15 Aug	fruit pod	1.0c
Pod apex	25 Aug	fruit pod	0.9
Pod	25 Aug	fruit pod	1.2
Pod apex	28 Aug	fruit pod	1.2c

[a] % of dry matter.
[b] flower or pod apex = entire raceme including flower or pod, petiole and stem material.
[c] TAC determined according to method of Cundiff and Markunas (1955), as modified by Williams and Cronin (1963).

Table 4. Percent of bites during 3 periods[d] by cattle grazing larkspur-infested mountain rangeland.

	Days			
Item	1-9 (Early)	10–18 (Mid)	19-27 (Late)	Overall
Larkspur				
leaf	0.2a	5.5b	15.4c	7.0
stem	0.1	te	t	t
pod	1.0a	5.8b	5.0b	3.9
flower	1.2a	1.9a	tb	1.3
total	2.5a	13.2b	20.4c	12.0
Graminoids	20.5a	15.3ab	13.7b	16.5
Other forbs[f]	76.6a	70.9ab	65.1b	70.9
Shrubs	0.2a	0.5a	0.8a	0.4

[abc] Values in the same row with a common letter have overlapping 95% confidence intervals.
[d] Complete data sets (morning and afternoon observations for all animals) were available for 27 days. For this table the study was divided into 3 periods of 9 days each.
[e] t = trace (<0.1%).
[f] Includes *Artemisia ludoviciana* and *Lupinus alpestris*.

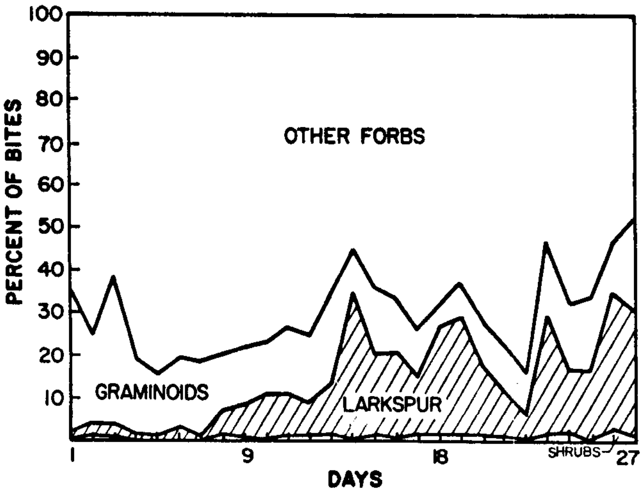

Fig. 1. *Percent of bites of tall larkspur, grasses, shrubs and other forbs taken by cattle on Utah mountain rangeland. Some days were deleted from the 30 July to 2 September trial because of incomplete observations for some animals.*

larkspur (Fig. 1). The selection of larkspur plant parts also changed over time. Cattle selected increasing amounts of larkspur leaf as the study progressed, and consumption of pods peaked midway in the trial and leveled off at about 5% of recorded bites (Table 4). Flower consumption was steady but very low (<2%) during the early and middle periods, and virtually disappeared as a dietary item by the end of the study.

Cattle consumed large quantities (>70% of bites) of other forbs during the study. Such forb consumption was unexpected because cattle are generally thought to be grass-preferring bulk and roughage eaters (Van Soest 1982). Preferred forbs were mountain dandelion, plantain, bluebells (*Mertensia* spp.), wild pea (*Lathyrus* spp.), and meadow rue. Graminoid consumption averaged 17% of bites overall, and decreased over time (Table 4). Consumption of

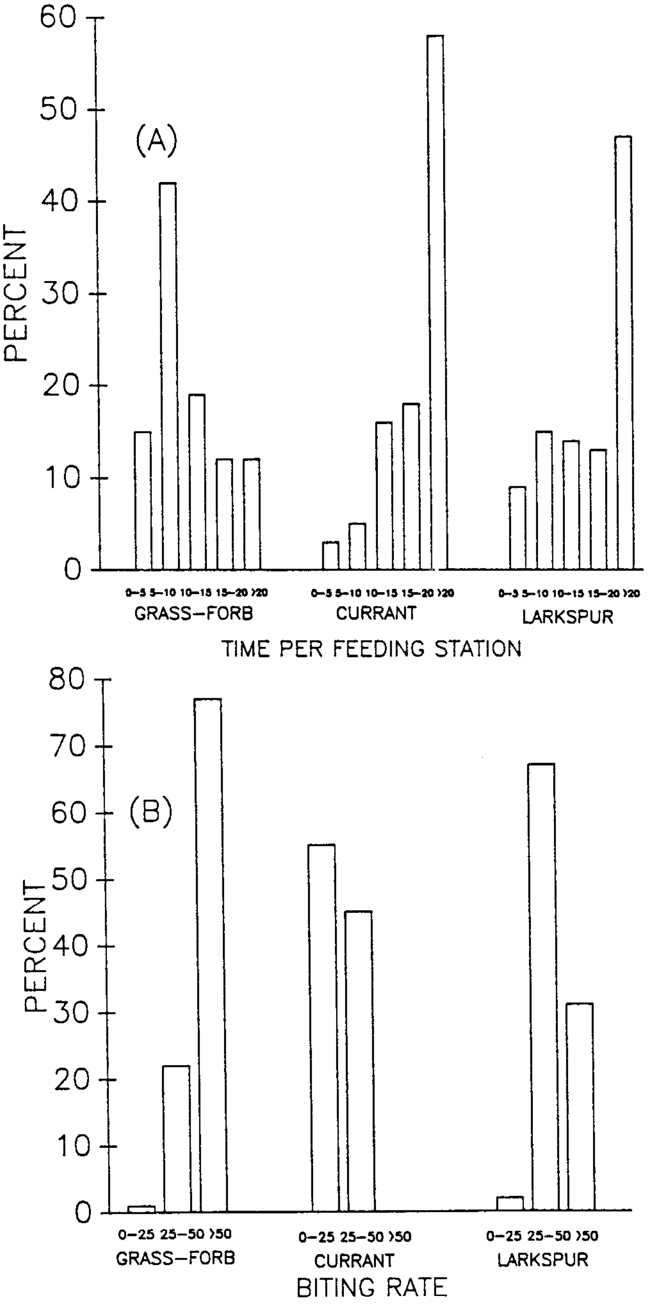

Fig. 2. *Histograms relating proportion (%) of (a) feeding station observations and class intervals (time spent per feeding station in seconds), and (b) biting rate observations and class intervals (bites/min) for 3 vegetation areas grazed on mountain ranges by cattle.*

Table 5. Means of behaviorial variables for cattle grazing larkspur rangelands by date and by vegetation area.

	Date				Vegetation		
	8 Aug	14 Aug	24 Aug	3 Sep	Grass-Forb	Currant	Larkspur
Time per feeding station (sec)	11.3a	13.8a	15.2ab	19.2b	11.2a	25.9b	22.0b
Bite rate (bites/min)	53.2ab	57.0b	56.7b	49.4a	64.4a	25.5b	46.0c
Step rate (steps/min)	79.1a	95.0a	85.8a	90.5a	91.5a	78.8b	86.8ab

[a,b,c] Means in the same row for dates or vegetation area with a common letter have overlapping 95% confidence intervals.

tall larkspur was negatively correlated with availability (kg/ha) of other forbs (excluding *Artemisia* and *Lupinus*) ($r = -0.62$, $P = 0.0001$) but not availability of graminoids ($r = -0.14$, $P = 0.15$).

Anecdotal accounts of tall larkspur poisoning of cattle frequently mention a relationship between cattle deaths attributed to larkspur and rainfall events (Glover 1906). Correlations between the percent of larkspur bites and the previous 12- and 24-h precipitation (mm) had r-values of 0.14 and 0.23, respectively. Correlations between larkspur bites and daily maximum and minimum temperature and relative humidity gave r-values of –0.24, –0.12, –0.08, and 0.13, respectively. It is interesting to note, however, that larkspur consumption by the cattle increased after the first 2 recorded rainshowers on days 8 and 9 of the study following a dry period of several weeks. Later peaks in larkspur consumption were not consistent with rainfall patterns.

Feeding Stations

Time spent per feeding station (TFS) was influenced significantly by vegetation area where the animals were foraging ($X^2=13.7$, d.f.=8, $P<0.001$) (Fig. 2). Most feeding stations in the grass-forb area were of 5 to 10-second duration. Feeding stations were relatively long (>20 seconds; Table 5) in both the currant and larkspur areas. There was no change ($P>0.05$) noted in TFS in grass-forb or currant areas over time. However, there was an increase ($P<0.05$) in mean TFS for observations made in the larkspur areas from 11.0 seconds on 14 Aug. to 24.0 seconds on 1 Sept. In virtually all cases, animals were grazing on larkspur plants in larkspur areas as TFS observations were taken. Conversely in the currant area, cattle generally were eating forbs underneath the currant bushes, and rarely browsing the currant shrubs. There was a trend of increasing ($P<0.05$) TFS as the study progressed when averaged over all vegetation areas (Table 5).

Biting rate (bites/min) differed significantly by vegetation area also ($X^2=363.0$, d.f.=4, $P<0.0001$) (Fig. 2). Cattle increased biting rate while grazing the grass-forb area, and most feeding stations had rates of >50 bites/minute. As cattle probed under currant bushes for desirable forbs, biting rate was slow (25 bites/min). Biting rate while grazing the larkspur area was intermediate (25–50 bites/min). There was no significant trend ($P>0.05$) for increased biting rate over time (Table 5) even though the standing crop of graminoids and forbs besides larkspur declined (Table 1).

Animal movement rate (steps/min) differed by vegetation area ($P<0.05$) (Table 5). Cattle moved more rapidly while grazing the grass-forb area, slowest in the currant area, and intermediate in the larkspur area. No change ($P>0.05$) was detected in the step rate over time (Table 5). The grazing pattern of the heifers was similar throughout the study except during periods of heavy rainfall. Mean grazing time was 10 ha and 40 min. During a typical day the cattle grazed from 0200 to 0330, 0700 to 1035, 1340 to 1630, and 1830 to 2115 h.

Behavioral data indicated that cattle grazed more rapidly (i.e., higher bite rate and step rate) while in the open-grass forb areas. The bite rate:step rate ratio can be considered a crude index of foraging efficiency. Thus cattle grazed most efficiently in the grass-forb areas, least efficiently in the currant areas, and intermediate in the larkspur areas.

Discussion

Cattle consumed little tall larkspur during the initial days of the study, but bites of tall larkspur increased gradually to 15 to 30% by late August. Increased consumption of leaves was particularly notable, and coincided with a decline in leaf alkaloids with increasing plant maturity. Pod consumption appeared to be more a function of availability than of level of alkaloids, as pod apex TAC continued to increase over time.

TAC's found in this study were lower than those reported previously (Williams and Cronin 1966, Laycock 1975, Olsen 1978). Williams and Cronin (1966) found TAC in leaves of duncecap larkspur (*D. occidentale* S. Wats.) of 1.6% on 5 Aug. and 1.2% on 26 Aug. Alkaloid levels in apexes of duncecap larkspur were found to be of >2.0% during August. Work currently underway will determine year-to-year variation in TAC at this study site. The influence of variation of TAC on consumption of tall larkspur or on cattle deaths is not presently known.

Olsen (1978) collected tall larkspur of various growth stages and reported total alkaloid content of >2.0% on a whole-plant basis. He reported that a median lethal dose (LD$_{50}$) for cattle of this material was 2.48 g of larkspur per kg of body weight. Representative tall larkspur bite sizes (dry weight) in our study were 0.2 g for leaves, 0.8 g for flowering racemes, and 1.0 g for pod apexes. The maximum daily ingestion rate of tall larkspur we observed was 8,320 bites (80% leaves, 20% pods). Over the course of this grazing day the cattle would then have ingested about 3.0 kg of tall larkspur (1.33 kg leaves and 1.67 kg pods). Calculation from Olsen's (1978) study (TAC levels 2.2%, animal weights 160 kg) indicate that LD$_{50}$ would have been about 0.9 kg of dry material. Had the tall larkspur in our study contained a higher concentration of alkaloids, this maximal number of bites would probably have been fatal, assuming higher alkaloid levels did not deter grazing.

There is much interest in plant secondary compounds as deterrents against herbivory (Provenza et al. 1987). Work at this laboratory indicates that cattle can be successfully averted from eating tall larkspur (Olsen and Ralphs 1986; Ralphs, unpublished data). On day 2 of this study, one heifer rapidly ingested a substantial but unknown quantity of tall larkspur, and was visibly distressed several hours later. Although this animal did not eat any tall larkspur for several days when her grazing cohorts were eating minor amounts, she subsequently began eating tall larkspur and provided no evidence of natural aversion.

Coley et al. (1985) have given a theoretical framework for relating herbivory, secondary plant compounds in plants, and environmental variables such as resource availability. This hypothesis relates high resource availability with high growth rate, relatively low levels of defense, and high rates of herbivory. Tall larkspur appears to fit this hypothetical framework, but empirical evidence is presently lacking. The hypothesis of Coley et al. (1985) will provide a background for future investigations with tall larkspur. In addition, we hypothesize that toxicity (and palatability) of *D. barbeyi* are related to plant phenology, as Olsen (1983) has indicated for *D. occidentale* toxicity using a mouse bioassay. Our observations indicate that tall larkspur is only palatable to most cattle after flowering. This is also when alkaloid concentrations begin to decline (Williams and Cronin 1966). Future work will also investigate factors triggering "gluttonous consumption", whereby individual animals reportedly graze large and fatal quantities of larkspur when the plant is presumably high in alkaloids. Much work remains to be done to elucidate plant/animal factors involved in tall larkspur toxicosis.

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Successional patterns in bitterbrush habitat types in north-central Washington

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Abstract

Twenty-five plant communities were classified within 3 bitterbrush *(Purshia tridentata)* habitat types along the Columbia River in north-central Washington. Topography, indicator species, and soils data were used to assign stands to habitat type. Ordination across 3 habitat types reflected a moisture gradient: bitterbrush/Idaho fescue *(Festuca idahoensis)* communities occupied the moist end, bitterbrush/needle-and-thread *(Stipa comata)* communities the xeric end, and bitterbrush/bluebunch wheatgrass *(Agropyron spicatum)* an intermediate position. Solar radiation index and elevation accounted for 76% of the variation in the major axis. Ordinations of communities within habitat types described the sere. High-seral communities were not present on the study area. Mid-seral communities had greater perennial grass cover and lower bitterbrush density than low-seral communities.

Key Words: bitterbrush, *Purshia tridentata*, plant successionclassification, ordination

Secondary plant succession patterns in forest habitat types are relatively well documented and ungulate use of forest seral stages has received a good deal of research attention (Miller 1968, Wallmo et al. 1972, Peek et al. 1976, Regelin and Wallmo 1978, Singer 1979, Wallmo 1969, Collins and Urness 1983, Irwin and Peek 1983). In contrast, secondary successional sequences in rangeland habitat types have received much less attention. Only recently (Huschle and Hironaka 1980, Hacker 1983) has a classification and ordination procedure for seral communities within rangeland habitat types been presented and evaluated. To date, the most detailed level of resolution in studies of ungulate use of rangelands has been at the habitat type or series level (Mackie 1970). To our knowledge ungulate selection of seral stages within rangeland habitat types has not been quantitatively addressed.

In order to evaluate mule deer preference for seral stages within rangeland habitat types, we needed to delineate the secondary successional sere within important habitat types and to determine whether a complete sere was available to mule deer on our study area. We chose to evaluate antelope bitterbrush habitat types because bitterbrush is one of the most palatable and nutritious browse species in western North America (Smith and Hubbard 1954, Kufeld et al. 1973), is known to be preferred by mule deer (Carson and Peek 1986), and because natural succession and disturbance have led to decreases in bitterbrush production and changes in understory composition throughout its range (Ferguson and Medin 1983). Although climax communities of bitterbrush habitat types have been described (Daubenmire 1970) no delineation of seral communities is available.

The purposes of this paper are: (1) to determine the relationship between topographic and edaphic site factors and bitterbrush habitat types, (2) to determine if established multivariate analysis tech-

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niques can effectively delineate the sere within bitterbrush habitat types, and (3) to provide summary descriptions of bitterbrush seral communities.

Study Area

The study area was part of the southern shore of an impounded segment of the Columbia River between Chief Joseph Dam and Grand Coulee Dam in north-central Washington. Elevations range from 300 m at the lakeshore to 900 m at the top of the canyon. The lake banks are a series of nearly level to gently sloping river terraces interspersed by long steep escarpments.

The climate is semiarid with cold winters and warm, dry summers. Most of the 240 mm mean annual precipitation falls as rain outside the growing season. Droughty summers have a great effect on the vegetation of the region (Daubenmire 1970).

Daubenmire (1970) recognized 3 bitterbrush habitat types in this area: bitterbrush/Idaho fescue *(Festuca idahoensis)*, bitterbrush/needle-and-thread *(Stipa comata)*, and bitterbrush/bluebunch wheatgrass *(Agropyron spicatum)*. All 3 habitat types are included within the big sagebrush *(Artemisia tridentata)*/bluebunch wheatgrass and threetip sagebrush *(Artemisia tripartita)*/Idaho fescue vegetation zones (Daubenmire 1970). Bitterbrush communities comprise approximately 25% of the study area.

The study area was a single pasture spring-fall range for 1,000–1,250 cattle. This grazing regime had been in effect for about 10 years prior to the study.

Methods

We selected 3 study sites of 280, 382, and 585 ha that included the range in elevation, slope, and vegetation composition of bitterbrush stands in the canyon. Bitterbrush stands were delineated on 8 inch-to-the-mile (1:660) black-and-white aerial photographs and stratified according to slope and aspect.

Five strata were identified. The first consisted of relatively flat stands with slope >4 degrees. Stands with >4 degrees slope on northern, southern, eastern, and western aspects comprised the remaining 4 strata. Sample stands were randomly chosen within strata.

We located a 20 × 20-m macroplot in each sample stand in an area of relatively uniform vegetation. Species presence, frequency of occurrence, and forb and grass canopy cover estimates were recorded from forty 20-by-50-cm microplots located at 2-m intervals along four 20-m-long transects placed parallel to the slope. Shrub cover was estimated using the line intercept method (Canfield 1941). Starting points for each transect were randomly located within successive 5-m intervals. Bitterbrush density was estimated from twelve 5-m^2 circular plots (Oldemeyer 1980) systematically located along the line intercept transects in each macroplot.

Elevation, slope, and aspect were recorded for each macroplot. Solar radiation index (SRI) was calculated from latitude, aspect, and slope (Frank and Lee 1966).

A soil pit was excavated to the C horizon in each macroplot. Soil was collected from each horizon. Soils were classified to family and series levels (USDA Soil Conservation Service 1975, USDA Soil Conservation Service 1981).

Sampled stands were assigned to habitat types based on topography, indicator plant species, and soil classification. Vegetative data were utilized to classify communities within habitat types using two-way species indicator analysis (TWINSPAN, Hill et al. 1975, Hill 1979a). Since this method is sensitive to rare species (Gauch and Singer 1982), forb and grass species present in <10% of the microplots per stand were eliminated from the analysis. Shrubs with canopy coverage of <3% were also deleted. Classification was based on presence or absence of species.

Plant communities identified by TWINSPAN were ordinated on the basis of canopy coverage within and among habitat types using detrended correspondence analysis (DECORANA, Hill 1979b, Hill and Gauch 1980). This ordination technique is based on reciprocal averaging and has been successful in community analysis (Gauch 1982; but see Wartenberg et al. 1987).

Ordination of communities can effectively identify seral relationships provided that all analyzed communities come from the same habitat type and a logical endpoint for succession is incorporated in the analysis (Huschle and Hironaka 1980, Tueller and Blackburn 1974). Climax communities sampled by Daubenmire (1970) in the vicinity were incorporated in the ordinations as reference stands for each of the habitat types. Hacker (1983) demonstrated the validity of reciprocal averaging methods to identify seral relationships in both simulated and real communities. DECORANA is an improved form of reciprocal averaging (Hill and Gauch 1980).

Cover estimates from sampled stands were averaged within communities. Stepwise multiple regression (Draper and Smith 1966, SAS Institute 1985) was utilized to aid in the interpretation of axes in the ordinations across all habitat types. Statistical analyses of differences ($P \leq 0.10$) in vegetation characteristics among habitat types and between seral stages were conducted with ANOVA of rank transformed data (Conover and Iman 1981). Pairwise comparisons were conducted with the Bonferroni approach (Miller 1966:67) at alpha = 0.10, experiment-wise.

Results

The 3 habitat types were located on distinctive topographic positions within the study area. Bitterbrush/needle-and-thread was found on relatively flat terrace benches (<4 degrees slope), bitterbrush/Idaho fescue was located on north facing slopes >4 degrees, bitterbrush/bluebunch wheatgrass was established on all other exposures with slope >4 degrees. Soils on all sites were derived from glaciofluvial deposits and were almost all sandy, sandy skeletal or loamy skeletal Typic or Entic Haploxerolls. "Cashmere", "Benge", "Skaha", "Pogue", and "Quincy" were the soil series encountered on the study area. Mollic epipedons were 15 to 36 cm thick over weakly developed cambric B horizons.

Soils were not as useful as topographic position in distinguishing habitat types. Needle-and-thread soils could not be visually differentiated from bluebunch wheatgrass soils. However, needle-and-thread is often found on sandier sites than bluebunch wheatgrass (Hironaka et al. 1983). Fescue soils were distinctive due to their darker color indicating a greater organic matter content.

The classification yielded 11 communities from the 41 stands sampled in the bitterbrush/bluebunch wheatgrass habitat type, 6 communities from 16 stands sampled in the bitterbrush/needle-and-thread habitat type, and 8 communities from the 22 stands sampled in the bitterbrush/Idaho fescue habitat type. These classifications were based primarily on the presence or absence of perennial forbs. Presence of bitterbrush and perennial grasses had little influence on community classification. Stands that had been burned in a 1981 wildfire were not separated from unburned stands in the classification. Communities therefore included both burned and unburned stands. Communities were named for the species with the greatest percent canopy coverage in the shrub, grass, and forb layer (Table 1).

The ordination across habitat types utilizing 28 communities represented an environmental gradient of all bitterbrush types on the study area (Fig. 1). SRI plus elevation accounted for 76% of the variation in axis 1. More mesic fescue sites were cooler, higher elevation communities located at one end of the ordination. Needle-and-thead sites were the warmest and driest communities at the opposite end. The bluebunch wheatgrass sites were intermediate between the other two. Bitterbrush cover and perennial grass cover accounted for 40% of the variation in axis 2.

Perennial grass cover in all communities in all habitat types sampled was much less than in reference climax stands (Table 1). Perennial forb cover in bitterbrush/bluebunch wheatgrass and bitterbrush/Idaho fescue habitat types was also much less than in

Table 1. Percent canopy coverage of perennial grasses, annual grasses, perennial forbs, annual forbs, and bitterbrush, and bitterbrush density for 28 bitterbrush communities in 3 habitat types, northcentral Washington, 1985.

Habitat type									
Community							Bitterbrush		
Number	Name	Seral stage	Burned[a]	Perennial grass cover (%)	Perennial forb cover (%)	Annual grass cover (%)	Annual forb cover (%)	cover (%)	Density (plants/ha)
	Putr/Agsp[b]								
1	Agsp/Basa	Mid	+	23.2	4.5	20.6	0.8	0.9	3250
2	Putr/Agsp/Basa	Mid	+	23.9	11.9	4.6	3.2	3.3	4500
3	Putr/Agsp/Basa	Mid	+	20.2	11.8	13.2	0.9	7.9	8625
4	Putr/Agsp/Basa	Mid	+	18.9	10.6	34.5	0.7	3.0	3000
	Mid-seral Average			21.6	9.7	18.2	1.4	3.8	4844
5	Putr/Agsp/Basa	Low		4.9	10.3	35.4	2.7	12.2	9429
6	Sado/Spcr	Low	+	14.5[c]	2.6	10.5	1.5	0.0	6000
7	Putr/Brte/Ardr	Low	+	2.2	7.7	24.1	0.5	8.0	6667
8	Putr/Brte/Erst	Low	+	1.5	5.6	25.6	1.3	9.7	11500
9	Putr/Brte/Libu	Low		6.0	12.6	26.6	1.6	7.0	45000
10	Putr/Brte/Basa	Low		6.2	6.7	29.2	14.7	12.2	12333
11	Putr/Brte/Loam	Low		2.5	6.7	34.6	3.6	7.9	7000
	Low-seral Average			5.4	7.5	26.6	3.7	8.1	13990
	Putr/Agsp Average			11.3	8.3	23.5	2.9	6.6	10664
	Putr/Stco								
12	Putr-Chna/Stco/Lepu	Low		9.6	3.9	27.7	1.4	5.6	12500
13	Putr/Stco-Spcr/Basa	Low	+	13.1	5.5	49.2	0.6	8.7	16667
14	Putr/Stco/Phha	Low		19.7[d]	1.9	22.8	2.3	22.0	26545
15	Putr/Stco/Libu	Low	+	9.1	7.0	20.5	9.7	11.3	11500
16	Putr/Stco/Acmi	Low	+	4.8	2.5	25.4	0.6	12.7	20000
17	Putr/Stco/Lule	Low		23.8	8.4	18.8	0.8	6.3	6000
	Putr/Stco Average			13.4	4.9	27.4	2.6	11.1	15535
	Putr/Feid								
19[e]	Feid-Agsp/Erhe	Mid	+	31.9	21.1	11.1	1.8	0.5	3333
20	Prvi/Feid-Agsp/Pogl	Mid	+	32.8	23.8	18.5	0.9	0.0	1000
21	Putr/Feid-Agsp/Erhe	Mid	+	18.5	24.9	23.2	5.4	9.6	8500
22	Putr/Feid-Agsp/Basa	Mid		17.7	16.3	7.2	3.0	12.9	11000
23	Putr/Feid-Agsp/Basa	Mid		22.8	20.3	12.0	0.5	8.1	5667
24	Putr/Feid-Agsp/Basa	Mid		27.1	20.2	4.1	0.2	9.4	8600
25	Putr/Feid-Agsp/Basa	Mid		27.5	18.7	1.2	0.0	6.2	4000
26	Putr/Feid-Agsp/Basa	Mid		39.4	23.4	1.0	0.2	4.6	4000
	Putr/Feid Average			27.2	21.1	9.8	1.5	6.4	5762
	Climax Reference[f]								
27	Putr/Agsp	High		88.0	32.0	1.0	9.0	11.0	—
28	Putr/Stco	High		78.0	3.0	5.0	15.0	12.0	—
29	Putr/Feid	High		98.0	91.0	2.0	12.0	25.0	—

[a] +denotes communities with at least one burned stand.

[b] Acmi=*Achillea millefolium*, Agsp=*Agropyron spicatum*, Ardr=*Artemisia dracunculoides*, Basa=*Balsamorhiza sagittata*, Brte=*Bromus tectorum*, Chna=*Chrysothamnus nauseosus*, Erhe=*Eriogonum heracleoides*, Erst=*Eriogonum strictum*, Feid=*Festuca idahoensis*, Lepu=*Leptodactylon pungens*, Libu=*Lithophragma bulbifera*, Loam=*Lomatium ambiguum*, Lule=*Lupinus leucophyllus*, Pogl=*Potentilla glandulosa*, Putr=*Purshia tridentata*, Prvi=*Prunus virginiana*, Phha=*Phacelia hastata*, Sado=*Salvia dorrii*, Spcr=*Sporobolus cryptandrus*, Stco=*Stipa comata*.

[c] Sand dropseed *(Sporobolus cryptandrus)* accounted for 97% of perennial grass cover.

[d] Needle-and-thread grass *(Stipa comata)* only accounted to 21% of perennial grass cover.

[e] Community Number 18 could not be assigned to a habitat type and was deleted from the analysis.

[f] Daubenmire (1970) communities #79,22,77.

respective reference climax stands. Mean bitterbrush density in Idaho fescue was lower (P=0.003) than in the needle-and-thread habitat type. In the Idaho fescue type mean perennial grass cover was higher ($P = 0.002$, $P = 0.012$) and mean annual grass cover was lower ($P = 0.002$, $P = 0.005$) than in bluebunch wheatgrass and needle-and-thread habitat types, respectively. Perennial forb cover differed ($P \leq 0.026$) among all habitat types. There was no significant variation among habitat types in annual forb ($P = 0.404$) or bitterbrush ($P = 0.324$) cover.

The first 2 axes of the community ordinations within habitat types accounted for 41 to 63% of community variation. Eigenvalues for axes 3 and 4 were quite small. In the bitterbrush/bluebunch wheatgrass habitat type axis 1 encompassed more than 3 standard deviations in species turnover. Axis 1 represented a secondary successional sere because the reference community (Daubenmire 1970) appeared at one end of the ordination. Com-

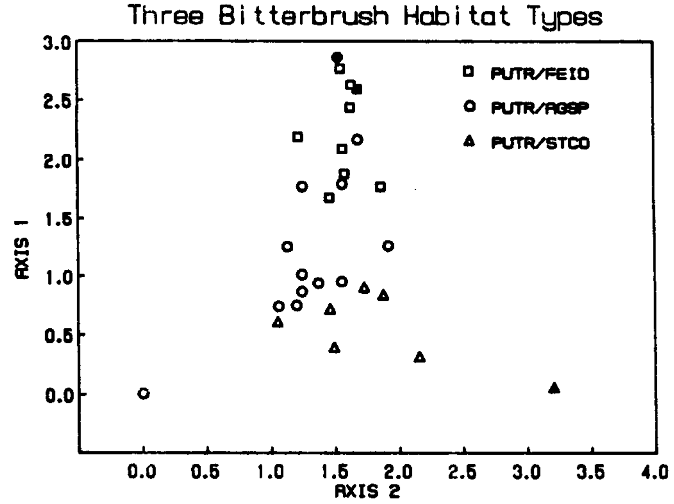

Fig. 1. *DECORANA ordination of 28 bitterbrush communities across 3 habitat types; PUTR/AGSP=bitterbrush/bluebunch wheatgrass, PUTR/FEID=bitterbrush/Idaho fescue and PUTR/STCO=bitterbrush/needle-and-thread. Solid symbols represent reference communities (Daubenmire 1970).*

munities with highest perennial grass cover appeared near the reference stands. Communities with least perennial grass cover were located far from the reference communities on axis 1. Communities were assigned to mid- or low-seral status (Table 1) based on a difference ($P<0.001$) in perennial grass cover because this was a readily observable criterion which has management utility. Low-seral communities had greater ($P = 0.086$) bitterbrush density than mid-seral communities (Table 1). Axis 2 accounted for only a small amount of variation.

In bitterbrush/needle-and-thread and bitterbrush/Idaho fescue a secondary successional gradient was not obvious. Ordinations in these 2 habitat types encompassed less than 2 standard deviations in species turnover, and a clear dichotomy in percent perennial grass cover within habitat type was not evident (Table 1). Because bitterbrush/Idaho fescue communities had consistently high perennial grass cover and bitterbrush/needle-and-thread communities had variable but generally low perennial grass cover, all communities in each of these habitat types were classed as mid-seral and low-seral respectively.

Discussion

Our ordination across habitat types identified an environmental gradient that can be used to evaluate wildlife habitat selection in rangelands. The habitat types occurred along an increasingly cooler and moister gradient from bitterbrush/needle-and-thread through bitterbrush/bluebunch wheatgrass to bitterbrush/Idaho fescue. This gradient of bitterbrush habitat types is consistent with Daubenmire's (1970) descriptions. By determining SRI and elevation from topographic maps and identifying bitterbrush stands from aerial photos or ground reconnaissance, land managers can map bitterbrush habitat types when the herbaceous layer is too disturbed to allow accurate habitat type assignment. Topographic data and soil properties can also be valuable in predicting habitat type of other grass or shrub communities (Anderson 1956, Tisdale and Bramble-Brodahl 1983).

In none of the habitat types on the study area did we observe communities approaching the pristine condition of reference climax communities; therefore a complete sere was not available in any habitat type. A similar situation would be expected on most low precipitation and low elevation rangelands with a history of grazing by non-native herbivores. Community variation in bitterbrush/Idaho fescue and bitterbrush/needle-and-thread habitat types was low and no seral separation would be made in these habitat types. The bitterbrush/Idaho fescue communities were located on steep north slopes not often utilized by livestock (Ganskopp and Vavra 1987). These sites either escaped prolonged grazing or were able to recover quickly from such disturbance due to a more favorable moisture regime; they were classed as mid-seral due to relatively high perennial grass cover. The bitterbrush/needle-and-thread communities were found on low elevation flat terrace benches that were close to water and historically received the greatest grazing pressure. Needle-and-thread grass cover in these communities was generally low, the grass layer was dominated by cheatgrass *(Bromus tectorum)*, and all communities in this habitat type were classed as low-seral.

Only in the bitterbrush/bluebunch wheatgrass habitat type did we observe 2 relatively distinct seral levels. Communities in this habitat type occurred on a variety of slopes, aspects, and elevations and had variable perennial grass cover. Most of the communities classed as mid-seral were found in areas with only moderate summer and fall cattle grazing; low seral communities were located predominantly in areas with heavy spring livestock grazing.

Within habitat type ordinations of communities were effective in objectively identifying the presence or absence of seres available for selection by mule deer. Delineation of seres provided an ecological framework which enhances our ability to predict long term changes in plant communities and to evaluate mule deer habitat selection relative to vegetation dynamics in rangelands. A similar approach could be used with other wildlife species in other rangeland types.

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Correction on Murray Article

A second Table 2 was erroneously included in "Response of three shrub communities in southeastern Idaho to spring-applied tebuthiuron" by Robert Murray on page 17 of the January issue. My apologies to the author.—The Editor

The influence of climate and soils on the distribution of four African grasses

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Abstract

Around 1900 temperate and semidesert grassland productivity declined, soil erosion increased, and drought destabilized the livestock industry in the northern and southern hemispheres. As government leaders throughout the world began to recognize the importance of grassland productivity and soil conservation, a massive experiment began to evolve. Government and private individuals collected seed from every continent, and planted seed at experimental stations and ranches in their respective countries. Hundreds of individuals who conducted thousands of seeding trials observed that buffelgrass (*Cenchrus ciliaris* L.), weeping lovegrass [*Eragrostis curvula* (Schrad.) Nees], kleingrass (*Panicum coloratum* L.), and Lehmann lovegrass (*Eragrostis lehmanniana* Nees) plants from seed collected in Africa were easier to establish and persisted longer than other grasses. Between 1930 and 1986 scientists in many countries evaluated the establishment and persistence of these grasses, but no attempt was made to synthesize the data base and determine the effects of climate and soil on plant establishment and persistence. Our objective was to: (1) determine the climatic and edaphic characteristics of areas where the seed of each grass was collected in Africa, and where each grass has been successfully established in both hemispheres, and (2) identify characteristics which influence long-term persistence. Where buffelgrass predominates and spreads, summer rainfall varies from 150 to 550 mm, winter rainfall is less than 400 mm, mean miminum winter temperatures rarely fall below 5° C, and soil texture is loamy. Weeping lovegrass can be established and plants persist when spring, summer, and fall rainfall varies from 400 to 1,000 mm on deep sandy soil and mean minimum winter temperatures rarely fall below -5° C. The invasion of adjacent nonplanted sites occurs only in Africa where growing season rainfall infrequently cycles between 750 and 1,000 mm and soils remain wet in mid-summer. Kleingrass can be established where mean maximum daily summer temperatures are above 30° C, mean minimum daily winter temperatures rarely fall below 0° C, summer growing season rainfall varies from 400 to 990 mm, and soils are clayey or silty. Kleingrass, like weeping lovegrass, spreads to nonplanted sites only in Africa where a mid-summer drought does not occur. Lehmann lovegrass predominates and spreads only in southern Africa, southeastern Arizona, and northern Mexico when summer rainfall in 30 to 40 days exceeds 150 mm, and soil textures are sandy or sandy loam.

Key Words: buffelgrass, kleingrass, Lehmann lovegrass, weeping lovegrass, rangeland seeding, Northern and Southern hemispheres

Commercial and religious rivalries among the Dutch, English, Portuguese, and Spanish between 1450 and 1550 resulted in the establishment of shipping lanes and exploration of continental land boundaries. Coastal exploration was followed by colonization, and by 1900 European settlers and their livestock had occupied the seemingly endless temperate and semiarid grasslands of Africa, Australia, North America, and South America. As European man and domestic livestock numbers increased, there was a corresponding increase in weed and woody shrub densities, and grassland productivity declined (Sellers and Hill 1974, Cooke and Reeves 1976).

Between 1880 and 1930, frequent droughts occurred in Africa, Australia, and North America, and livestock numbers declined (Brooks 1929, Bogdan 1961, Cox et al. 1983a). In an attempt to stabilize livestock populations, botanists, ranchers, and military personnel from Australia, England, South Africa, and the United States travelled throughout the world searching for a "miracle grass" that could produce an abundance of good quality forage with limited precipitation. Attempts were also made to develop high-producing varieties through plant breeding that would surpass native species (Thornber 1905). Their approach was to: (1) collect seed from plants growing in harsh environments, (2) plant seed at experimental stations or ranches in their respective countries, (3) increase seed from species that appeared to be drought tolerant, and (4) plant seed under extreme climatic and edaphic conditions (Griffith 1901). From thousands of seeding trials conducted throughout the world, 4 warm-season African grasses were recognized for their ease of establishment, persistence, and forage production. The grasses were buffelgrass (*Cenchrus ciliaris* L.), weeping lovegrass [*Eragrostis curvula* (Schrad.) Nees], kleingrass (*Panicum coloratum* L.), and Lehmann lovegrass (*Eragrostis lehmanniana* Nees). The purpose of this paper is: (1) to determine where the original seed sources were collected, and by whom; (2) to determine where the 4 grasses have been successfully established from sown seed, where mature plants have persisted for more than 20 years, and where seed from mature plants has colonized new areas; (3) to discuss relationships between climate, soils, and pests which may influence the long-term persistence of the 4 grasses; and (4) to evaluate the results as they may apply to future seedings throughout the northern and southern hemispheres.

Materials and Methods

Historical records and journals were examined to determine (1) where seed were originally collected and (2) countries where each grass had been successfully established. Rangeland conservationists in each country provided estimations of the area sown to each grass as well as adjacent colonized areas.

Climatic and edaphic data were collected at or from nearby areas where seed were originally collected and where mature plants established from seed persisted for 20 or more years. Climatic reporting stations were selected based upon (1) topographic similarities between reporting stations and the area where seed were collected or established, and (2) having 10 or more years of continuous records which corresponded with actual planting or invasion years.

Climatic data are summarized in the following mean monthly categories: (1) maximum temperatures, (2) minimum tempera-

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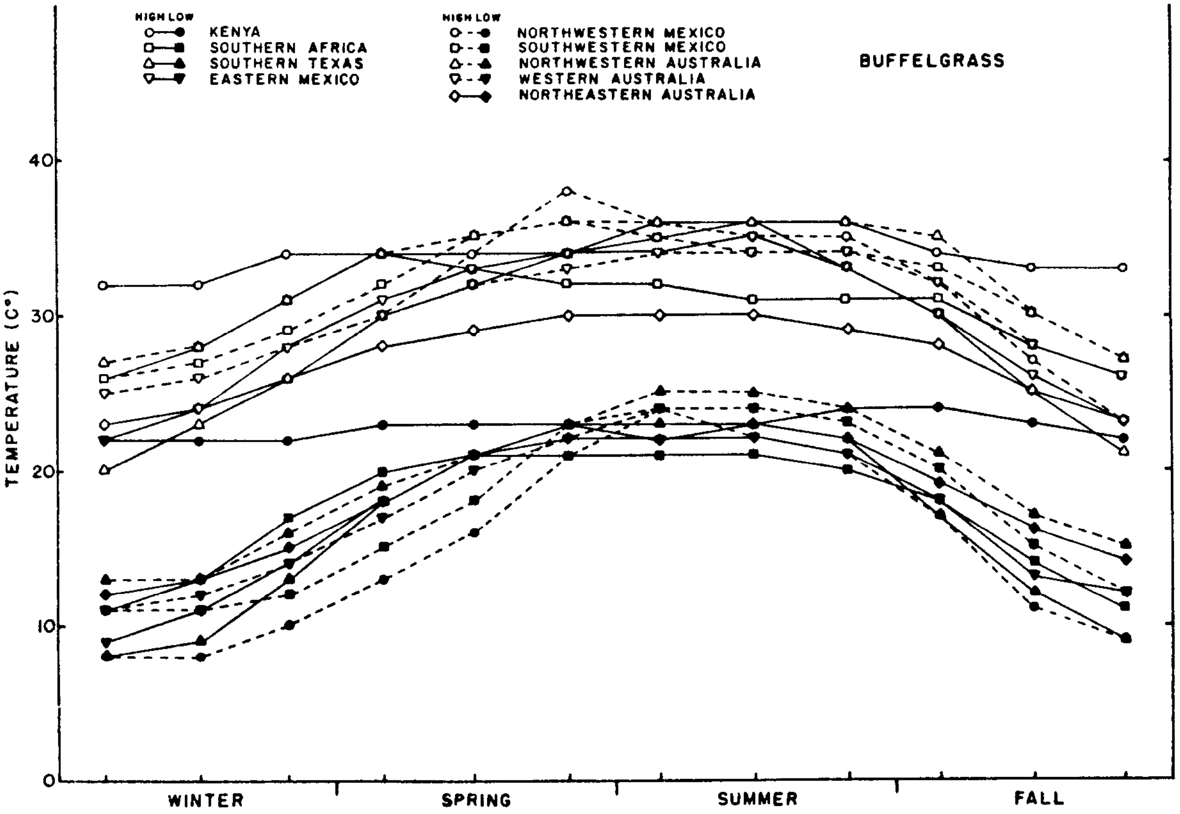

Fig. 1. *Mean monthly maximum and minimum temperatures during winter, spring, summer, and fall where buffelgrass has been successfully established in the northern and southern hemispheres.*

tures, and (3) precipitation. Data from stations in the northern and southern hemispheres are adjusted by month so that winter, spring, summer, and fall seasons correspond.

Results

Initial plant establishment from seed was documented in 31 countries for buffelgrass, 15 for weeping lovegrass, 9 for kleingrass, and 5 for Lehmann lovegrass. Long-term persistence and colonization, however, occurred only in 6 countries for buffelgrass, 3 for weeping lovegrass, 2 for kleingrass and 1 for Lehmann lovegrass.

Buffelgrass

C.J.J. van Rensburg, Department of Agriculture, South Africa, collected buffelgrass seed at many semiarid northeast African locations between 1940 and 1945. Seed were sown at Rietvlei Plant Introduction Station near Pretoria and evaluated for establishment, persistence, and forage production. Plants from seed collected in the Turkana Desert of northcentral Kenya and southern Ethiopia in 1940 survived a drought in 1942, and a seed production program was initiated in 1945.

Seed from the Turkana Desert collection were shipped to the United States in 1946 (Holt 1985). Plants were successfully established and persisted in southern Texas, and the U.S. Department of Agriculture, Soil Conservation Service (USDA-SCS) informally released T-4464 buffelgrass in 1949. Between 1949 and 1985, Texas seed producers sold 7 million kg of T-4464 seed, and ranchers in southern Texas established the grass on over 4 million ha. Seed were transported south into Mexico and successfully established on 6 million ha along the eastern coast, and on 300,000 ha along the western coast. T-4464 as well as seed from other buffelgrass collections made in Pakistan and southern Africa (Ivory et al. 1974) were shipped to Australia and successfully established on 7.5 million ha in the western and northern territories (Humphreys 1967).

Various buffelgrass accessions have been selected for production and cold tolerance (Das et al. 1978, Ivory and Whiteman 1978, Khan and Zarif 1982). Neither factor, however, can be repeatedly shown to differ among accessions when tests were conducted under the same or similar climatic and edaphic conditions.

Where buffelgrass occurs in northcentral Kenya and southern Ethiopia, elevations vary from 150 to 700 m, and mean monthly minimum and maximum temperatures annually vary from 21 to 24° C and 31 to 36° C (Fig. 1), respectively. Rainfall is bimodally distributed in 2 summer growing seasons, and annually varies from 200 to 400 mm. Buffelgrass is generally found growing in loam and sandy clay loam soils, and growth occurs whenever soil moisture is available (National Animal Husbandry Research Station Annual Report from Naivasha, Kenya 1979).

Where buffelgrass has been successfully established from seed, elevations vary from 6 to 830 m; but mean minimum winter temperatures at these locations are 10 to 15° C colder than in the Turkana Desert (Fig. 1). Leaf growth begins when mean minimum temperatures rise above 10° C. but active growth occurs only in summer when mean minimum temperatures are between 15 and 20° C and mean maximum temperatures are below 40° C in southern Africa (du Toit et al. 1973, Dye and Walker 1980), northeastern and northwestern Australia (Humphreys 1967, Sweeney and Hopkinson 1975, Harsh et al. 1981), eastern and western Mexico (Cota and Johnson 1975, Molina et al. 1976), and the southcentral United States (Hanselka 1985). Annual rainfall varies from 200 mm in the Turkana Desert and northwestern Mexico to 1,250 mm in northeastern Australia, and may be distributed in

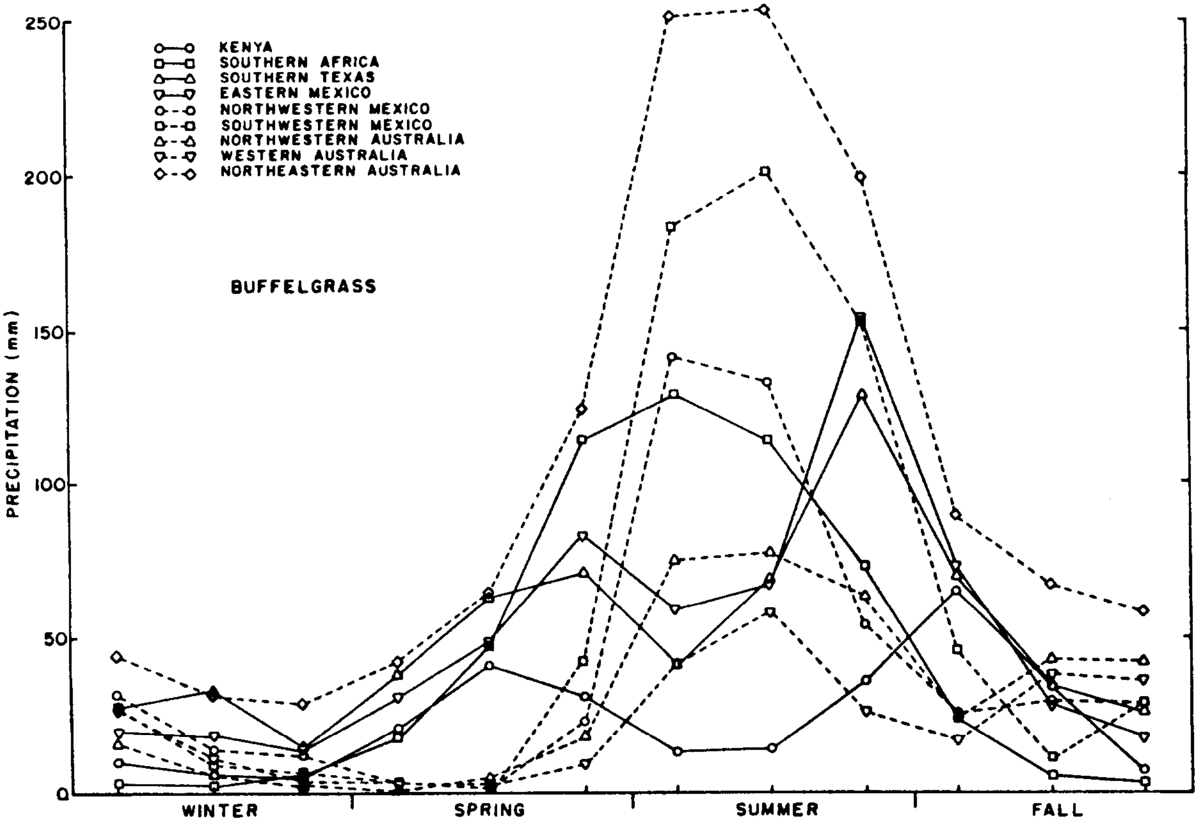

Fig. 2. *Mean monthly precipitation during winter, spring, summer, and fall where buffelgrass has been successfully established in the northern and southern hemispheres.*

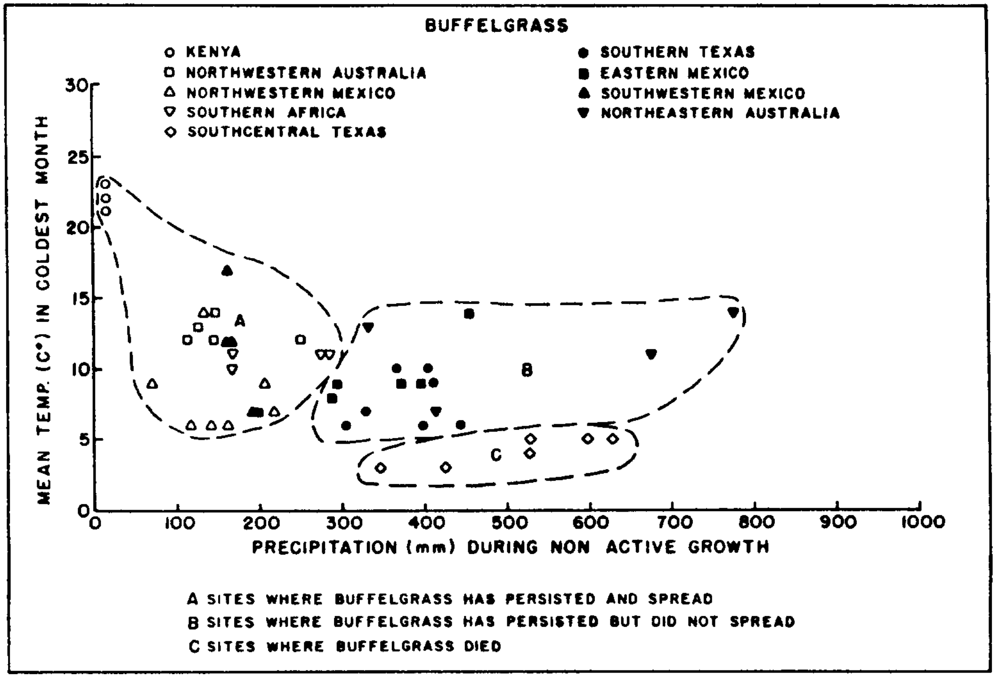

Fig. 3. *The effect of mean winter temperature and winter precipitation on the long-term persistence of buffelgrass in the northern and southern hemispheres.*

either a summer peak, bimodally in summer, bimodally in summer and fall or bimodally in summer and winter.

Buffelgrass seed, from plants established on planted sites, actively colonize adjacent nonplanted sites in Kenya, southern Africa, northwestern Australia, and northwestern Mexico. At all locations, summer rainfall during active plant growth varies from 170 to 400 mm while rainfall during dormancy varies from 10 to 285 mm (Fig. 2); dry periods totalling 150 to 210 days occur in either winter or in fall and spring; and mean minimum temperatures in the coldest month range between 0 and 23° C. Under such conditions, buffelgrass seed in soil may remain viable for 3 years (Winkworth 1963).

Established stands persist but do not actively colonize adjacent nonplanted sites in northeastern Australia, southwestern Mexico, eastern Mexico, and southern Texas. Summer rainfall exceeds 440 mm in northeastern Australia and southwestern Mexico, while rainfall during dormancy generally exceeds 300 mm in northeastern Australia, eastern Mexico and southern Texas (Fig. 2). Plant distribution under these environmental conditions is limited by allelopathy (Hussain and Ilahi 1982), competition with more productive forbs and grasses (Sweeney and Hopkinson 1975), insects which reduce plant vigor (Reis et al. 1984), and pathogens (Azmi and Singh 1985) which reduce seed germination during extended wet periods in either summer or winter.

In southcentral Texas, mean minimum temperatures in the coldest month are below 6° C, rainfall during dormancy generally exceeds 400 mm (Fig. 3), and an extended dry period does not occur. Stands established under these conditions fail to persist because seed produced in summer is destroyed during wet winters (Amzi and Singh 1985) and established plants die during cold winters (Holt 1985).

Weeping Lovegrass

L.W. Kephart and R.L. Piemeisel, Bureau of Plant Industry, U.S. Department of Agriculture, collected weeping lovegrass seed in northcentral Tanzania in 1927 (Crider 1945). Seed were collected from plants growing in black, waxy, sun-cracked soil on an escarpment between Mbula and Ngorongoro Craters, where elevation varied from 1,300 to 1,800 m.

Seed were shipped to Arizona in 1932 and numbered A-67 (Crider 1945). Weeping lovegrass was initially thought to be adapted in the semiarid southwestern United States, but mature plants were unable to survive spring and summer droughts (Bridges 1941, Judd and Judd 1976). Mature plants from seed planted in Oklahoma and northwestern Texas, however, did persist and between 1940 and 1980 A-67 weeping lovegrass was established on 800,000 ha.

In 1947 and 1953 seed from collections in Oklahoma were transported to Argentina and plants were established on 800,000 ha (Covas and Carinie 1985). Seed were also transported and established in southeastern Australia (Lloyd et al. 1983, Watt 1983), southern Africa (Kruger and Grunow 1983, Kategile 1985), Japan (Nada 1985), and Spain (Nieto 1985).

Three major weeping lovegrass types, selected for leafiness and cold tolerance, have been and are currently being compared to A-67. 'Morpa' (more palatable) was collected by R.K. Godfrey, Bureau of Plant Industry, U.S. Department of Agriculture, at Rietvlei Plant Introduction Station near Pretoria, South Africa in 1953. Seed were planted at Woodward, Oklahoma, in 1954, and seed from mature plants that survived in harsh winter in 1955–1956 were increased (Voigt 1971). 'Morpa' is taller, leaves are wider, and plants mature earlier than A-67 (Novosad et al. 1983). Beef cattle and sheep prefer 'Morpa' and gain weight faster than when grazing A-67 (Shoop et al. 1976).

'Ermelo', a leafy weeping lovegrass type was collected 200 km southeast of Pretoria at Nooitgedacht Research Station in 1944. Elevation is 1,750 m and nighttime temperatures are frequently below freezing in fall, winter, and spring. 'Ermelo' was introduced into the United States in 1948, and a second ecotype from an 'Ermelo' seeding in Zimbabwe was introduced in 1964.

Weeping lovegrass seeds collected from 54 sites in Basutoland (currently Lesotho) were increased by the Department of Agriculture and Technical Services in Pretoria and shipped to the United States in 1964. One selection, Renner, was more palatable and vigorous than the others. Renner has blue-green leaves and leaves are broader than A-67, 'Ermelo' and 'Morpa'. Renner was released in 1972 by the Texas Research Foundation (Read et al. 1980).

Differences among the 4 weeping lovegrass types, which do not include all African types, are related to leaf size, vigor, palatability

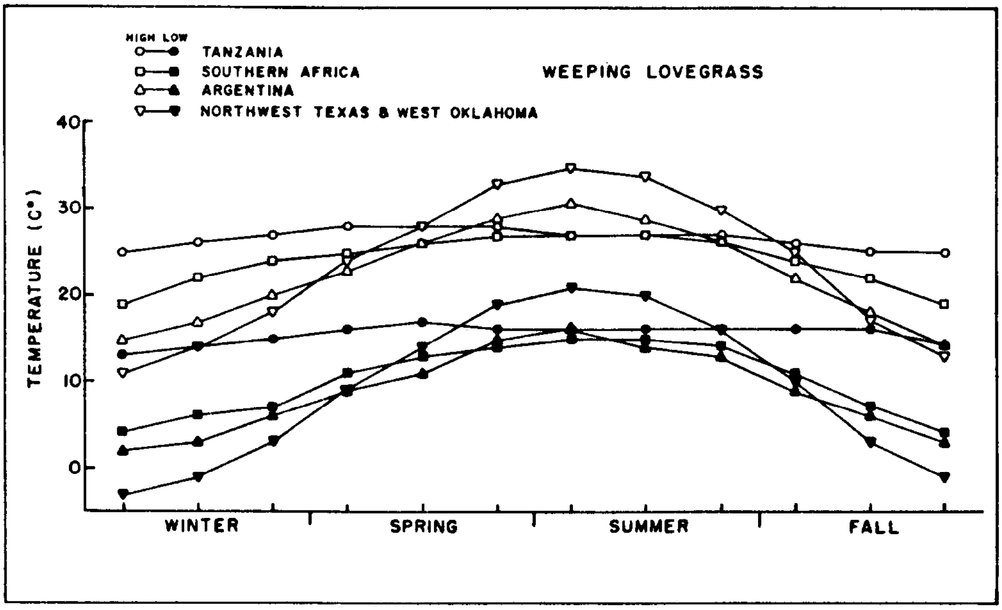

Fig. 4. *Mean monthly maximum and minimum temperatures during winter, spring, summer and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.*

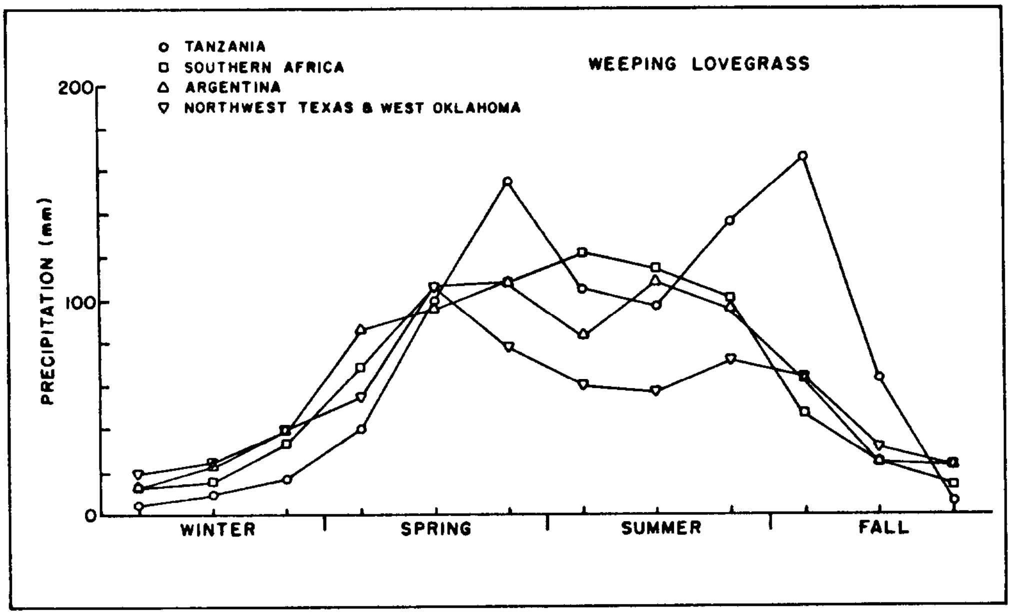

Fig. 5. *Mean monthly precipitation during winter, spring, summer, and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.*

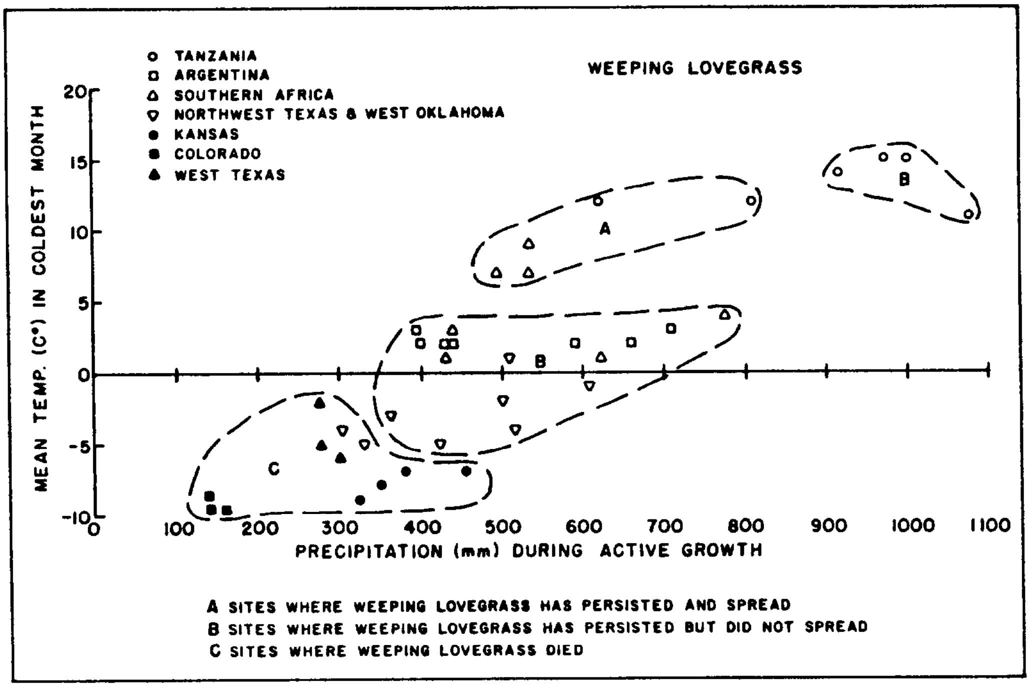

Fig. 6. *The effect of mean winter temperature and summer precipitation on the long-term persistence of weeping lovegrass in the northern and southern hemispheres.*

and possibly cold tolerance. The 4 types, however, represent most of the potential variability within the weeping lovegrass complex (Kruger and Grunow 1983). Thus, all types will be considered as 1 in our discussion.

In northcentral Tanzania where weeping lovegrass occurs, elevations vary from 1,190 to 1,530 m. Mean monthly minimum and maximum temperatures range from 10 to 18° C and 25 to 30° C, respectively (Fig. 4). Rainfall is bimodally distributed in summer and fall, and annually varies from 625 to 1,075 mm. More than 80% of the annual rainfall (765 to 965 mm) occurs when mean minimum daily temperatures are above 15° C, and winter and spring are typically cool and dry. Weeping lovegrass generally grows in deep sand or loamy sand. Leaf growth occurs when early summer rains begin, productivity peaks in mid-summer just prior to or during a moderate dry period, and regrowth occurs in fall (Mukurasi 1984).

Weeping lovegrass has been successfully established from seed in southern Africa, southcentral Argentina, and southcentral United States, but the species does not actively colonize adjacent nonplanted sites. In South Africa, on the Natal Highlands and northern Transvaal Plains, weeping lovegrass has been established at 700 to 1,750 m elevations, while in Argentina plants are most often established at 80 to 310 m elevations. Winters in Tanzania, South Africa, and Argentina are cold and dry (Fig. 4), but mean minimum winter temperatures in Tanzania are 8 to 10° C warmer than in South Africa and Argentina.

Rainfall in South Africa peaks in mid-summer and annually varies from 500 to 1,200 mm, while rainfall in Argentina peaks in early and late summer and annually varies from 640 to 955 mm (Fig. 5). Rainfall in the growing season ranges from 400 to 775 mm, at both locations, and mean maximum summer temperatures rarely exceed 30° C. Plant growth occurs when soil moisture is available and mean minimum temperatures rise above 10° C, and productivity peaks in mid-summer when mean minimum and maximum temperatures vary between 15 and 30° C (Kruger and Grunow 1983, Rethman and de Witt 1984, Covas and Cairnie 1985).

In the United States, weeping lovegrass has been established from southern Colorado to southern Arizona and from Maryland to Georgia (Crider 1945, Denman et al. 1953). Plant persistence, however, is limited to 300 to 1,000 m elevations in western Oklahoma, and northwestern and northcentral Texas. Plant growth begins in late spring when mean minimum temperatures rise above 10° C; productivity peaks when mean minimum and maximum temperatures range between 15 and 30° C; growth declines in mid-summer when mean maximum temperatures exceed 30° C and soils dry (Shoop and McIlvain 1970).

In western Oklahoma and northwestern and northcentral Texas, mean minimum daily temperatures in the coldest month vary from -1 to -5° C (Fig. 6) and minimum daily temperatures in winter are below 0° C for 60 to 90 days. Under such conditions established weeping lovegrass stands will persist if they are not fertilized and defoliated prior to freezing winter temperatures (Rommann and McMurphy 1974). To the north in southern Kansas and west in southeastern Colorado, mean minimum temperatures in the coldest month vary from -7 to -10° C and daily minimum temperatures are below 0° C for 120 to 160 days. Weeping lovegrass can be established during summer in Kansas and during atypically wet summers in Colorado, but plants die in winter (Dwyer et al. 1974, Dalrymple 1976, Shoop et al. 1976, Read et al. 1980, Novosad et al. 1983). Stands can also be established during atypically wet summers and they persist for 10 or more years in southern Arizona, eastern New Mexico, and west Texas; but mature plants die when summer rainfall declines to 350 mm (Bridges 1941, Judd and Judd 1976).

Weeping lovegrass has been used throughout the world to revegetate mine spoils and steep slopes (Cresswell 1973, Farrington 1973, Wang et al. 1975, Voigt et al. 1982). Established stands persist where summer rainfall varies from 400 to 1,000 mm, and mean minimum and maximum temperatures annually vary from 0 to 30° C. Plant production, however, declines where summer rainfall exceeds 75[illegible] mm because of allelopathy (Dalrymple and Rogers 1983), competition with other forbs and grasses (Giraudo et al. 1984), fungal infections (van der Merwe et al. 1979), mites (Ehara 1985), and nematodes (Gnanapragasam 1981, van den Berg 1985).

Kleingrass

Dr. Mildred Wilman, Director of the McGregor Museum, Kimberley, South Africa, collected kleingrass seed between Kimberley in the Orange Free State and Potchefstroom in the Transvaal in 1949. Seed from the collections were planted throughout Texas between 1954 and 1968. Plants were successfully established in central Texas, and in 1968 the USDA-SCS and the Texas Agricultural Experiment Station jointly released Selection 75 (Holt 1969).

Between 1975 and 1985, commercial seed producers in Texas sold over 2 million kg of Selection 75 seed, and seed were planted on 2.8 million ha of degraded rangeland. Seed were transported and established on small acreages in eastern Australia (Rees 1972), Brazil (Alberto and Barreto 1983), Cuba (Oquendo et al. 1983), India (Mukherjee 1972), Japan (Inosaka et al. 1975), Venezuala (Gallardo and Leone 1983) and Zimbabwe (Mills 1977).

Kleingrass variety *makarikariense,* originally collected in Botswana, has a bluish color and wider leaves than Selection 75 (Holt et al. 1985). *Makarikariense* has been successfully established on small acreages in eastern Australia (Lloyd et al. 1983), Brazil (Alberto and Barreto 1983), and Japan (Inosaka et al. 1975).

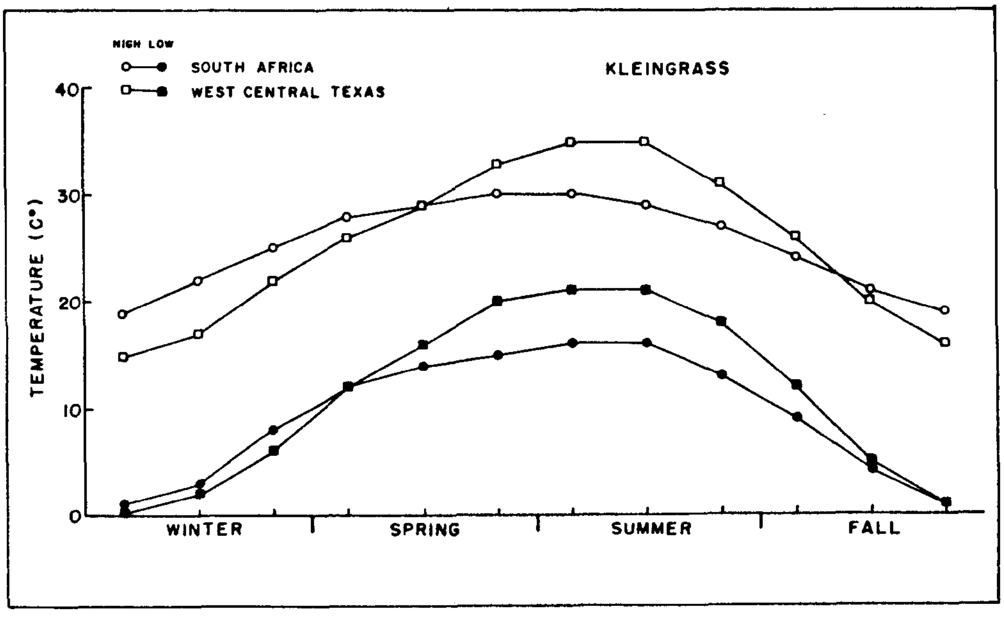

Fig. 7. *Mean monthly maximum and minimum temperatures during winter, spring, summer, and fall where kleingrass has been successfully established in the northern and southern hemispheres.*

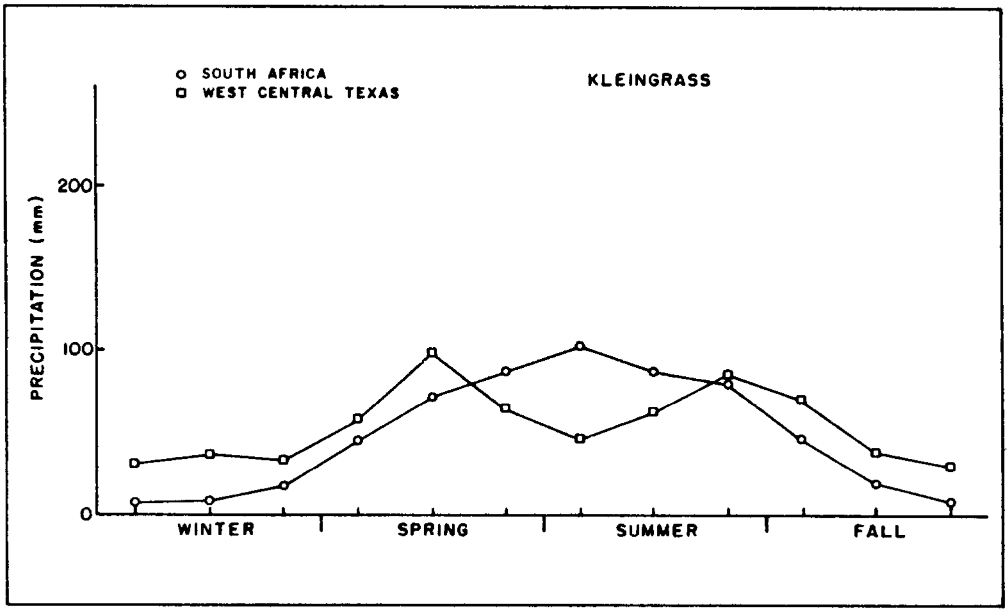

Fig. 8. *Mean monthly precipitation during winter, spring, summer, and fall where kleingrass has been successfully established in the northern and southern hemispheres.*

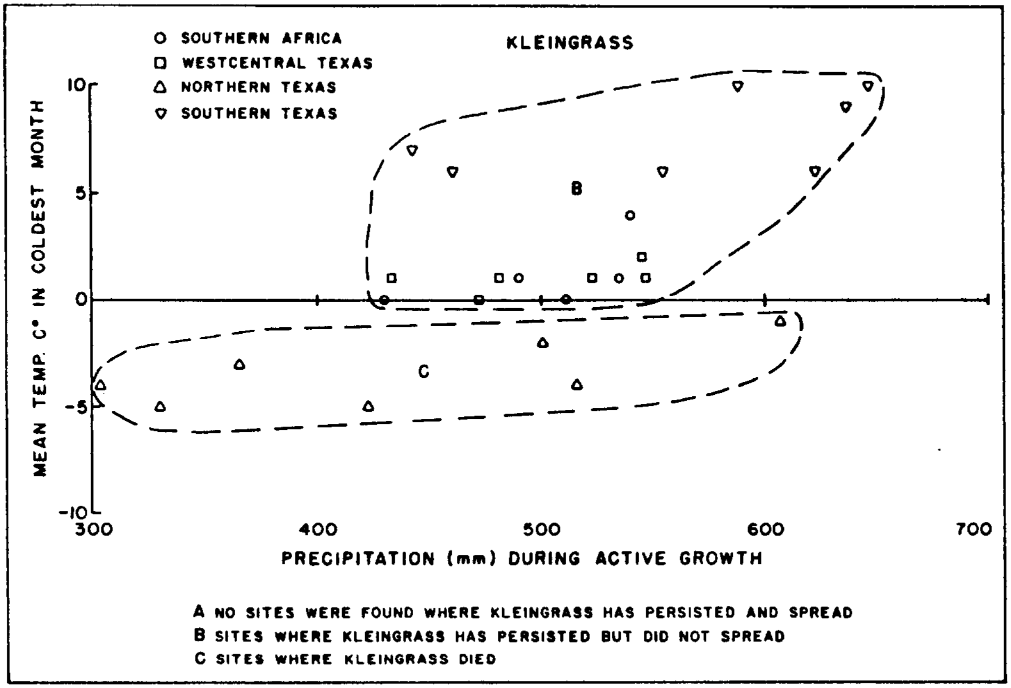

Fig. 9. *The effect of mean winter temperature and summer precipitation on the long-term persistence of kleingrass in the northern and southern hemispheres.*

Selection 75 is apparently more cold tolerant than *makarikariense*, but their establishment, productivity, and digestibility characteristics under moisture stress are similar (Kobayashi et al. 1978, MacKenzie et al. 1982, Bade et al. 1985). Thus, both selections are considered as one in our discussion.

Elevations in the western Transvaal of South Africa range from 1,000 to 1,450 m, and mean monthly minimum and maximum temperatures annually vary from -2 to 17° C and 16 to 31° C (Fig. 7), respectively. Rainfall peaks in summer, and annually varies from 425 mm at Kimberley to 610 mm at Potchefstroom. Winters are dry, and mean minimum daily temperatures in the coldest month vary from -5 to 4° C. In Zimbabwe, 200 to 300 km north, kleingrass grown under a similar climatic regime initiated growth in spring when temperatures approached 10° C and moisture in the soil was available (Rodel and Boultwood 1981). Plant productivity peaked when mean daily minimum and maximum temperatures ranged from 15 to 30° C, and seedlings and mature plants were most often found where fine soil particles and water accumulated (Rodel 1972).

Kleingrass has been successfully established from seed in Australia (Rees 1972), Brazil (Alberto and Barreto 1983), Japan (Kobayashi et al. 1978), United States (Holt 1969), Venezuela (Gallardo and Leone 1983) and Zimbabwe (Rodel 1972), but the species does not actively colonize adjacent nonplanted sites. The species can be expected to survive extreme fall defoliation only in west central Texas (Holt et al. 1985) and southern Africa (Rodel and Boultwood 1981).

In west central Texas, elevations range from 440 to 540 m, and mean minimum and maximum temperatures annually vary from 0 to 22° C and 12 to 36° C (Fig. 7), respectively. Winters are dry in some years while wet in others, and mean minimum daily temperatures in the coldest month vary from 0 to 2° C. Rainfall is bimodally distributed, and peaks occur in late spring and early fall (Fig. 8). If soil moisture is available kleingrass grows from spring to fall when mean minimum daily temperatures are above 10° C. Plant productivity peaks throughout summer when mean maximum temperatures range from 30 to 36° C (Stubbendieck et al. 1973, Pitman and Holt 1983, Bade et al. 1985, Bedunah and Sosebee 1985). Weeping lovegrass productivity, under similar temperature extremes, rapidly declines even when soil moisture is available (Farrington 1973, Mills 1977, Covas and Cairnie 1985).

Kleingrass persistence is limited by temperature to the north and by precipitation west of west-central Texas (Taliaferro et al. 1983), while production is limited by competition to the east and south (Holt et al. 1985). Established kleingrass stands in northern Texas and Oklahoma die (Holt 1969) where mean minimum daily temperatures in the coldest month vary from -1 to -5° C (Fig. 9) and minimum daily temperatures in winter are below 0° C for 30 to 60 days; whereas in west Texas, stands die if total precipitation in the growing season (April to October) is less than 400 mm (Pratt et al. 1971). Kleingrass can be successfully established and will persist in high rainfall (700 to 990 mm) areas of east and south Texas, but competition with other seeded grasses reduces kleingrass forage production (Hussey and Holt 1982). Production in high rainfall areas may also be limited by nematodes (Rodel et al. 1976).

Toxins accumulate in kleingrass foliage, and goats and sheep may die after consuming large quantities during fall in southern Africa (Rodel 1972) and summer and fall in central Texas (Dollahite et al. 1977, Muchiri et al. 1980). The distribution of kleingrass, as a potential pasture grass, may be limited because of its toxic characteristics.

Lehmann Lovegrass

Dr. Mildred Wilman, Director of the McGregor Museum, Kimberley, South Africa, sent Lehmann lovegrass seed collected in the Griqualand West Region of South Africa to F.J. Crider at Superior, Arizona, in 1932 (Crider 1945). In 1935, Crider organized a series of irrigated screening tests at Tucson, Arizona, and selected plants that matured quickly and produced seed in the first growing season. Seeds from established plants were numbered A-68.

Between 1937 and 1950, approximately 135 kg of Lehmann lovegrass seed, produced at Tucson, was planted in small plots from west Texas to Arizona. Many of the seedings were successful, and between 1951 and 1985, commercial seed growers produced more than 75,000 kg of Lehmann lovegrass seed. Approximately 70% of the seed was sown on rangelands in Arizona, New Mexico, and Texas. The majority of the remaining seed was transported into Mexico and planted in the northern frontier states of Chihuahua, Coahuila, and Sonora (Cota and Johnson 1975, Sanchez 1976, Cox et al. 1984). Between 1940 and 1980, ranchers and government agencies successfully established Lehmann lovegrass on more than 70,000 ha and the species spread by seed to an additional 70,000 ha in the southwestern United States and northern Mexico (Cox and Ruyle 1986).

Elevations in west-central South Africa where Lehmann lovegrass occurs naturally, range from 1,175 to 1,350 m and mean minimum and maximum temperatures annually vary from 0 to 19° C and 18 to 34° C (Fig. 10), respectively. Annual rainfall peaks in late summer, and approximately 80% (225 to 395 mm) is distributed in late spring, summer and early fall when mean minimum daily temperatures are above 15° C. Rainfall amounts are low and storms are widely distributed in late spring and summer, and

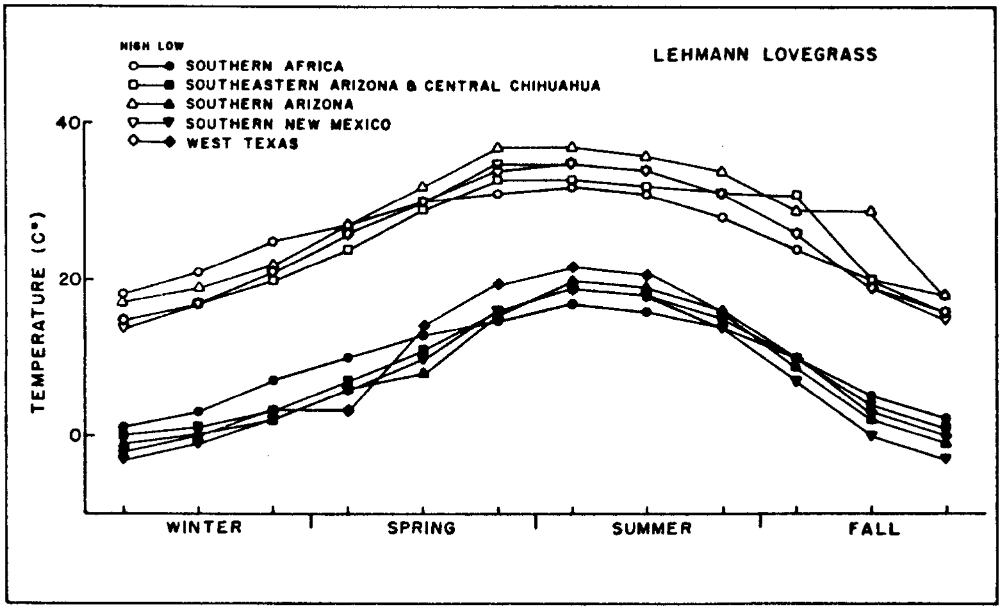

Fig. 10. *Mean monthly maximum and minimum temperatures during winter, spring, summer and fall where Lehmann lovegrass has been successfully established in the northern and southern hemispheres.*

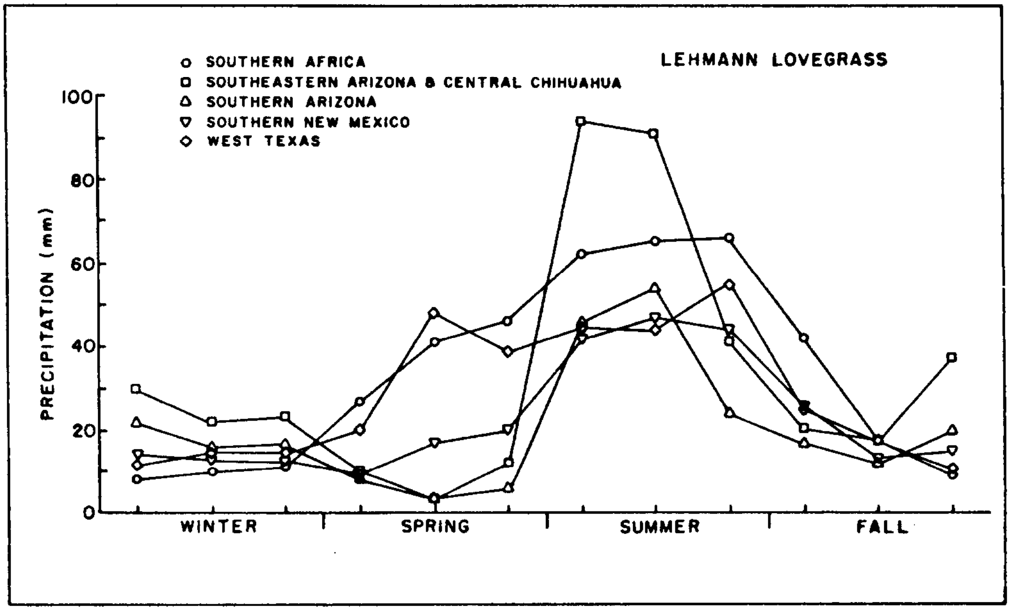

Fig. 11. *Mean monthly precipitation during winter, spring, summer and fall where weeping lovegrass has been successfully established in the northern and southern hemispheres.*

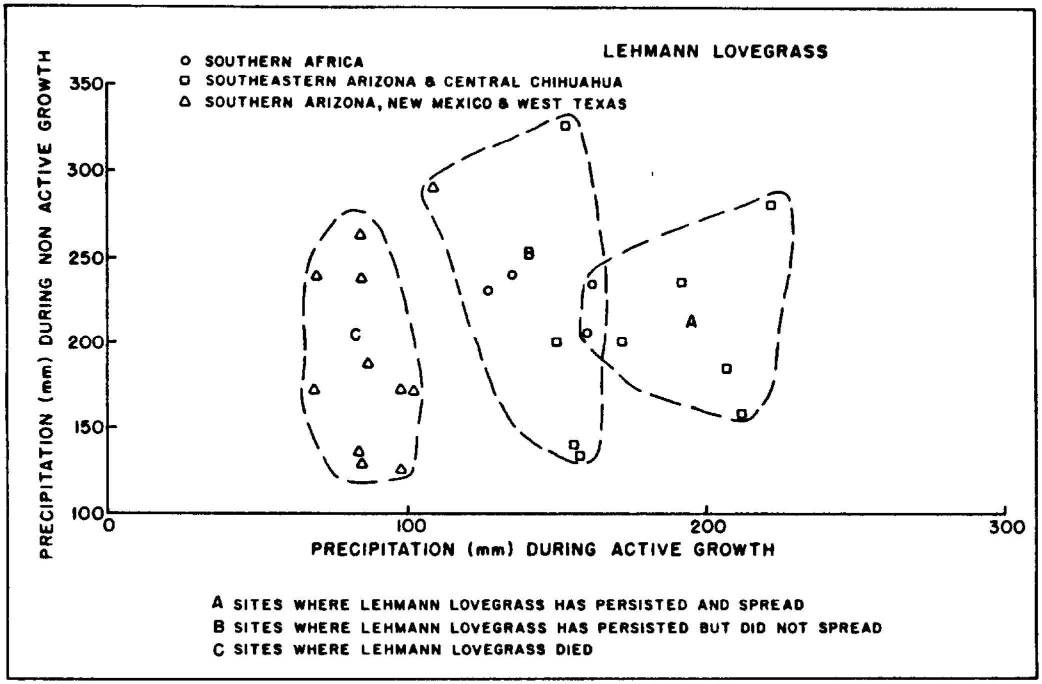

Fig. 12. *The effect of winter and summer precipitation on the long-term persistence of Lehmann lovegrass in the northern and southern hemispheres.*

Lehmann lovegrass normally remains semidormant. As rainfall amount and distribution increase in late summer, Lehmann lovegrass initiates growth and productivity peaks in 30 to 40 days (Fourie and Roberts 1976). Precipitation during active growth ranges from 130 to 160 mm (Fig. 11) while mean minimum and maximum temperatures vary from 15 to 32° C.

Where Lehmann lovegrass has been successfully established and has spread in the southwestern United States and northern Mexico, elevations range between 775 and 1,540 m, and daily mean minimum and maximum temperatures vary annually from -4 to 20° C and 13 to 38° C, respectively (Fig. 10). Annual rainfall varies from 275 to 500 mm, and may be distributed in a summer peak or bimodally in summer and winter (Fig. 11).

Lehmann lovegrass seed, from plants established on planted

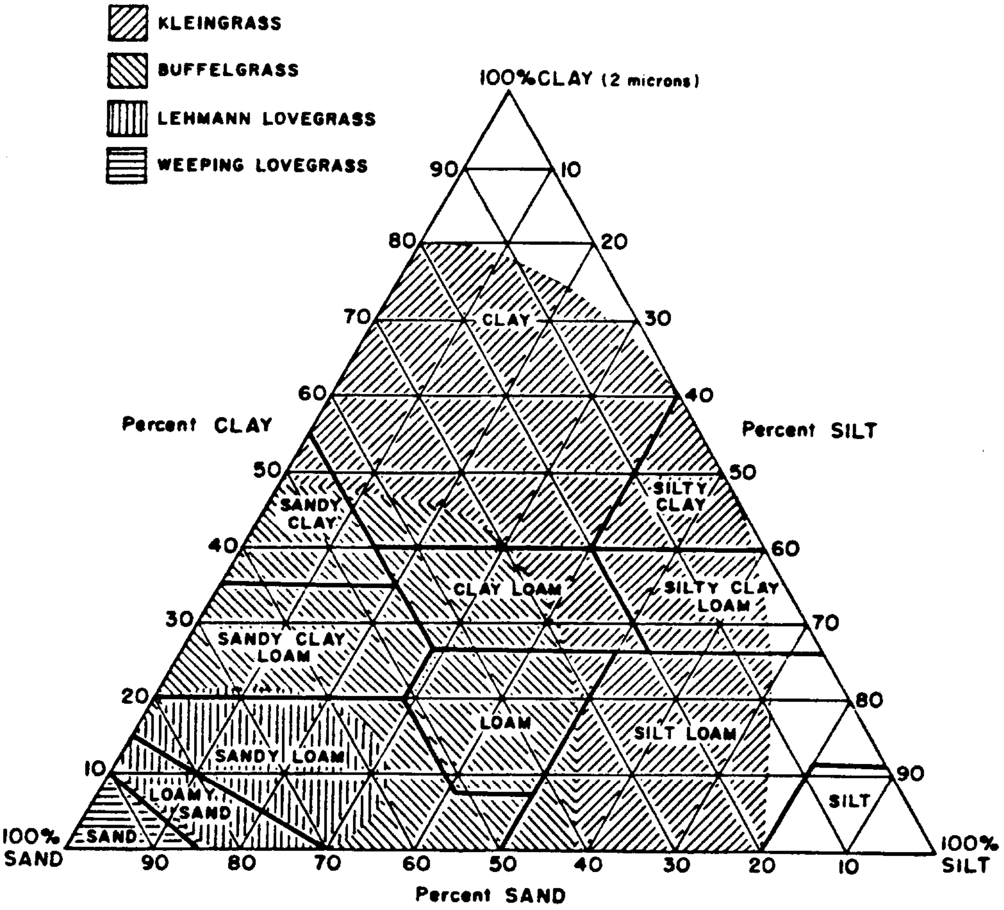

Fig. 13. *The effect of soil texture on the long-term persistence of four warm-season African grasses.*

sites, actively colonize adjacent nonplanted sites in southeastern Arizona (Cox and Ruyle 1986) and northcentral Mexico. At all locations, summer rainfall during active plant growth ranges from 150 to 220 mm (Fig. 12), and elevations vary from 1,100 to 1,540 m (Anderson et al. 1957, Cable 1971). Where Lehmann lovegrass has persisted but has not spread in southeastern Arizona, southern New Mexico, west Texas, and northern Mexico, summer rainfall during active growth is about 100 mm. Established Lehmann lovegrass stands in the area die when summer rainfall during active growth ranges between 70 and 85 mm.

Effects of Soil Texture

Buffelgrass, kleingrass, weeping and Lehmann lovegrasses have been initially established in almost all soil textural types; but long-term persistence of each grass is dependent on specific textural types (Fig. 13). Buffelgrass and kleingrass seedlings emerge when seed are sown in sandy, silty, and clayey soils, but buffelgrass emergence declines as either sand, silt, or clay content approaches 100% (Mutz and Scifres 1975, Agostini et al. 1981). Buffelgrass seedlings gradually lose vigor and die when established in silt, silt loam, silty clay loam, silt clay and clay soils; whereas, kleingrass seedlings persist in the same soils (Sweeney and Hopkins 1975, Watt 1976, Christie 1978, Pitman et al. 1981, Rodel et al. 1981, Hanselka 1985). Buffelgrass persists in well-drained loam, sandy loam, clay loam, and sandy clay loam soils, and actively spreads by seed in northwestern Australia and northwestern Mexico in sandy loam soils (Humphreys 1967, Cota and Johnson 1975).

Weeping lovegrass seedlings emerge from sand, loamy sand, sandy loam, and loam soils, but long-term persistence in southern Africa is normally, but not always, limited to deep sandy soils (Rethman and de Witt 1984). Sand depth may vary from 1 to 5 m (Farrington 1973, Wang et al. 1975, Kruger and Grunow 1983), and the soil profile may be saturated seasonally (Covas and Cairnie 1985).

In the eastern and southern United States weeping lovegrass can be established and will persist in sandy soil (Dalrymple 1976, Haferkamp and Mutz 1982). Plant distribution in this area, however, is limited by soil texture which is predominantly silt loam, clay, and clay loam. Chemical and physical characteristics of these soil types either reduce or inhibit weeping lovegrass germination (Stubbendieck 1974), seedling emergence (Cox et al. 1986), shoot growth (Chichester 1981, Lavin et al. 1981), and root growth (Tischler and Voigt 1983).

Lehmann lovegrass seedlings emerge when seeds are planted near the surface in sand, loamy sand, and sandy loam soils; seedlings, however, do not emerge in silt loam, loam, and clay loam soils, regardless of planting depth (Cox et al. 1983b). In southeastern Arizona and northcentral Mexico long-term persistence and spread is limited to loamy sand and sandy loam soils (Cox and Ruyle 1986).

Discussion

Attempts to artificially revegetate degraded rangelands in the northern and southern hemispheres have been going on for approximately 100 years (Humphreys 1967, Cox et al. 1986). The method most widely used to establish grasses was to: (1) mechanically reduce unwanted competition, (2) prepare a seedbed, (3) plant seeds of as many species, accessions, and cultivars in as many soil types as possible, and (4) pray for rain. In 1 of every 10 planting attempts grasses were successfully established, but climatic and edaphic data were not collected and it was impossible to determine why plantings were either successes or failures.

When grasses were successfully established there was a tendency to extrapolate, because successes occurred infrequently, and imply that a species was adapted over a broad geographic region. Lehmann lovegrass can be established on most soils in the southwestern United States and northern Mexico in an atypically wet summer (Cox et al. 1984), but the species persists and spreads only on sandy or sandy loam soils where summer precipitation in 30 to 40 days varies from 150 to 220 mm (Cox and Ruyle 1986). Hence, Lehmann lovegrass is adapted at a few localized areas, rather than throughout the southwestern United States and northern Mexico.

The identification of climatic and edaphic factors which influence the persistence (Fig. 1-13) of the 4 African grasses can be used to predict where each grass is adapted. For example, the distribution of buffelgrass, kleingrass, and weeping lovegrass is limited when mean minimum temperatures in the coldest month are 5° C or less, or 0° C or less and -5° C or less, respectively, whereas, the distribution of Lehmann lovegrass appears to be limited by the amount and distribution of summer rainfall and soil texture rather than cold temperatures. Buffelgrass requires approximately 90 growth days in summer and relatively warm, dry winters to colonize loam soils, while Lehmann lovegrass requires 30 to 40 growth days in summer to colonize sandy loam soils. Kleingrass and weeping lovegrass can be established and mature plants will persist where the summer growing season varies from 120 to 150 days, but neither actively invades nonplanted sites except in Africa where the growing season approaches 180 days.

Prior to 1975 it was economically feasible to seed degraded rangeland because petroleum was inexpensive. After 1975 the cost of petroleum dramatically increased and a successful seeding in 1 of every 10 attempts was no longer a worthwhile investment. If mechanical treatment and seeding is to remain a range improvement practice the probability of success must be improved. Thus, information which defines the relationships among climate and soils, and plant germination, emergence, persistence and reproduction is essential. A successful range seeding cannot be guaranteed if climate and soil are considered when selecting grasses for revegetation, but it will reduce the probability of failure.

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Plant distribution surrounding Rocky Mountain pinyon pine and oneseed juniper in south-central New Mexico

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Abstract

Within the pinyon-juniper type, trees and understory vegetation are interspersed with open areas forming a mosaic of vegetational patterns. The objective of this research was to define and describe vegetational zones surrounding Rocky Mountain pinyon (*Pinus edulis* Engelm.) and oneseed juniper (*Juniperus monosperma* [Engelm.] Sarg.). Transects consisting of contiguous frames were laid out from the base of the tree and continued into the interspace area (outside the canopy) for each cardinal direction. Potential zone boundaries were located by calculating a squared Euclidean distance utilizing basal cover estimates of each frame. Zone boundaries were verified by discriminant analysis. Vegetation associated with both pinyon pine and oneseed juniper exhibited 3 zones. Zone 1 consisted of vegetation associated with the tree bole. Zone 2 was, for the most part, located beneath the tree canopy. Zone 3, consisting primarily of interspace, contained mostly perennial grasses and forbs. Mean basal cover of vegetation surrounding oneseed juniper increased from <1% in zone 1, to approximately 7% in zone 2, to about 12% in zone 3. Mean basal cover estimates of vegetation associated with pinyon pine increased from approximately 4% in zone 1, to 10 and 11% in zones 2 and 3, respectively. Differences in species composition among zones between tree species were apparent.

Key Words: vegetational patterns, understory composition, *Pinus edulis, Juniperus monosperma*

Within the pinyon-juniper woodland, trees and understory vegetation are interspersed with open areas forming a mosaic of vegetational patterns. While these patterns may be obvious to the careful observer, few quantitative evaluations of these gradients have been made. For example, Arnold et al. (1964) found rather drastic reductions in basal cover of grasses and forbs with increasing canopy cover. A similar trend was observed with herbage production.

Everett et al. (1983) studied vegetational patterns in a singleleaf pinyon *(Pinus monophylla)*-Utah juniper *(Juniperus osteosperma)* woodland. Basal cover decreased from north to west to south aspects (6.7, 3.7 and 1.9% respectively). In general, understory cover was displaced from the tree stem with increasing tree size and duff depth. Some species, however, were benefited by tree effects, and older trees with decreasing depth of duff, at times, appeared to allow undergrowth to recover. Peak undergrowth basal cover generally occurred in the vicinity of the duff boundary (increased vigor phase), and declined toward the tree bole (exclusion phase) and interspace (depletion phase). The authors point out, however, these patterns were variable among aspects and cross-slope, upslope, or down-slope transects.

Similarly, Everett and Koniak (1981) found cover highest in the transition microsite between duff under the canopy and bare ground interspace between trees. No significant differences in plant cover were found between the understory microsites and the interspace areas. Some species exhibited an affinity for certain microsites.

Clary and Morrison (1973) found cool-season species production higher (1.6 kg ovendry forage) beneath the canopies of mature and overmature alligator junipers (*Juniperus deppeana* Steud.), compared to only 0.36 kg for a treeless area equivalent in size.

Arnold (1964) delineated 4 distinct vegetation zones surrounding a oneseed juniper near Show Low, Arizona; Zone 1, next to the tree bole possessed no herbaceous vegetation. It received the least light and presumably the most moisture (via stemflow) of the 4 zones. The first zone surrounded the tree bole. Zone 2 produced 132.9 kg air-dry perennial grass and forb herbage per ha. This zone was located beneath the tree canopy, except for the northerly direction, where it extended approximately 2/3 m beyond the canopy edge. Snakeweed (*Gutierrezia sarothrae* [Pursh.] Britt. and Rushby.) had the greatest cover in the second zone, followed by western wheatgrass (*Elytrigia smithii* [Rybd.] D.R. Dewey). In contrast, zone 3 produced 86.1 kg/ha. Zone 3 consisted primarily of interspace, and continued to a distance of approximately 5.5 m. The absorption and depletion of soil moisture by root hairs of the juniper are thought to have prevented the full development of western wheatgrass and snakeweed in zone 3. Blue grama (*Bouteloua gracilis* [H.B.K.] Lag.) dominated this zone. Zone 4 produced

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215.5 kg per ha. This zone is presumably outside the influence of the juniper and consists of interspace. Snakeweed had its highest cover in this zone.

Johnsen (1962) noted, as the size of oneseed junipers increased, vegetation was increasingly excluded from the understory. However, as the tree senesced, its canopy become elevated and grasses and forbs were able to recolonize the understory.

No comparative studies have been conducted on the major dominant tree species of the pinyon-juniper woodlawns of central New Mexico. The objective of this study was to define vegetational zones surrounding Rocky Mountain pinyon and oneseed juniper.

Study Area

The Fort Stanton Experimental Ranch is between the Capitan and Sierra Blanca mountains of south-central New Mexico. Mean annual precipitation is 348 mm, 60% of which occurs during the growing season (Lymbery and Pieper 1983). Precipitation in 1985, until the time of sampling (June), was 74 mm, approximately 95% of the average for this time period. The average annual temperature is 11.1° C, with a mean minimum of -6.6° C occurring in January, and a mean maximum of 28.9° C occurring in July (Pieper et al. 1971). Winds are predominantly from the west and southwest (Lymbery and Pieper 1983).

Average elevation of the study site is 1,870 m. Slope is approximately 5% with a northwest aspect. Soils of the study site have been classified as a fine, loamy, mesic Aridic Haplustoll (Bailey et al. 1982). These areas were not grazed by livestock during this study.

Common grass species of the study area include blue grama (*Bouteloua gracilis* [H.B.K.] Lag.), wolftail (*Lycurus phleoides* H.B.K.), and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.). Major forbs include groundcherry (*Physalis* sp. L.), scarlet globemallow (*Sphaeralcea coccinea* [Pursh] Rydb.), and chamaesaracha (*Chamaesaracha coronopus* [Dunal] Gray) and the half shrub broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt & Rusby). The shrub layer is dominated by skunkbush sumac (*Rhus trilobata* Nutt.), algerita (*Berberis haematocarpa* Woot.) and an occasional wolfberry (*Lycium pallidum* Miers). Oneseed juniper (*Juniperus monosperma* Engelm. Sarg.), Rocky Mountain pinyon (*Pinus edulis* Engelm), and an occasional alligator juniper are the sole tree species of the area. Plant nomenclature follows Lebgue and Allred (1985).

Methods

Zonation

Twelve vigorous oneseed junipers relatively uniform in size (4-6m in height) and morphology were selected for study. In each of the 4 cardinal directions, forty 61.00 × 15.24-cm frames were placed from the tree base continuing into the interspace. An ocular estimate of basal cover (to the nearest whole percentage) for each species rooted within the frame was recorded during June 1985. Tree canopy width in each direction was also measured by using an imaginary line perpendicular from the outermost edge of the tree canopy and recording this distance from the tree bole.

Fifteen Rocky Mountain pinyon trees were also selected for study. These trees were in vigorous condition and were 100–150 years of age. For each tree, only as many suitable directions as were available were utilized. A direction was deemed unsuitable if at least 30 frames could not be placed without encountering the influence of another tree. (The edge of a pinyon's influence was assumed to extend 5 m beyond the canopy edge). Basal cover and canopy cover width were measured in an identical fashion to that for the juniper.

Potential vegetational zone boundaries were located by calculating a squared Euclidean distance, as described by Ludwig and Cornelius (1987), utilizing basal cover estimates of each frame. Basal cover estimates of adjacent frames were grouped into window widths along the transect data. A window corresponded to the data from at least 2 frames; windows can be set to any feasible number of frames. The window is then divided into two equal groups of transect data, and a squared Euclidean distance is calculated between these 2 groupings. The squared Euclidean distance formula indicates the difference between the basal cover estimates of each group on an individual species basis. If a species in one group is lacking, its value is set to zero. Differences are squared, repeated for all species within this window. The resulting values are summed, thereby yielding the squared Euclidean distance. The window is then moved one position, or frame, down the transect and another squared Euclidean distance is calculated. This process is continued until the window reaches the last frame along the transect and can be moved no further. A window width of 6 frames was used for this analysis (Fig. 1). This width was used because it tended to lessen, or dampen, the occurrence of peaks resulting from purely random noise compared to procedures utilizing smaller windows.

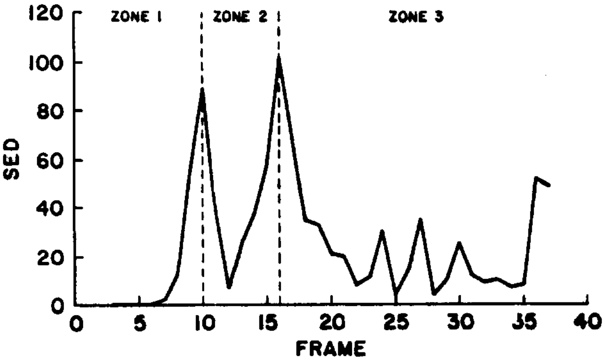

Fig. 1. *Squared Euclidean distance peaks across quadrats placed from tree bole to interspace utilizing a window width of 6 for a sample direction of representative tree.*

Initially, as many zones as there were major peaks were defined. Once potential zones were delimited, a discriminant analysis using species cover values was employed to test the zone classification. We examined understory species frequency along the transect and selected those species that exhibited a repeatable pattern of occurrence relative to the tree crown. We used discriminant analysis to test the correctness of the number of understory zones based on percentage of frames correctly classified. This process was continued until a high percentage of the frames were correctly classified. Squared Euclidean distance results for both species were similar (Fig. 1).

Basal cover data were subjected to analysis of variance using the Statistical Analysis System with an alpha set equal to 0.05 (SAS Institute 1982). When the analysis of variance indicated a significant difference among zones or directions, individual means were compared by least significant differences. In these analyses, individual trees were considered replications.

Results and Discussion

Three vegetational zones were identified surrounding both oneseed juniper and pinyon pine. Zone 1 around pinyon pine was clearly defined, while zones 2 and 3 were not as distinct, but were still relatively well-defined. Zones surrounding oneseed juniper were somewhat more clear.

Zone 1 of the juniper was located beneath the tree canopy and extended to a distance of approximately 1.0 m from the tree bole. Zone 2 approximated the juniper canopy edge and was roughly 2.1 m from the tree bole. Precise zone location, however, varied somewhat with direction (Fig. 2). Zone 3 consisted of some area beneath the canopy, but was mostly interspace. Results of the discriminant analysis for oneseed juniper are shown in Table 1. For example, 15

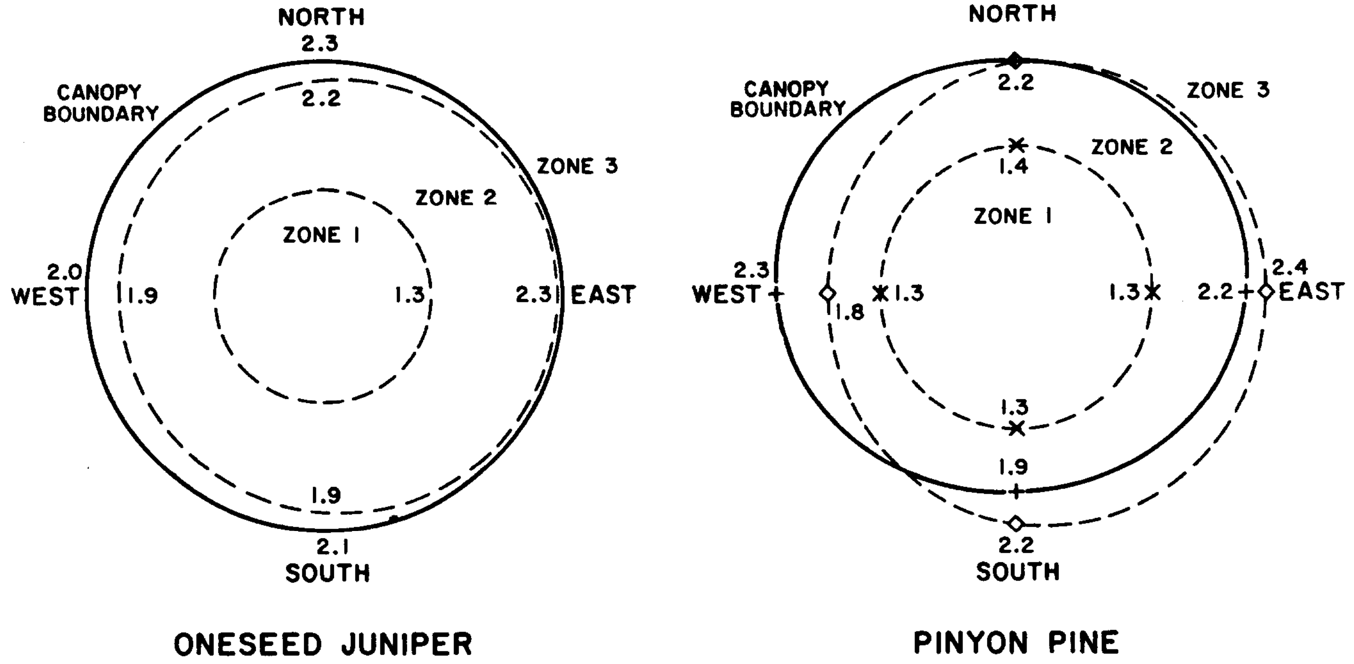

Fig. 2. *Vegetational zones and canopy boundaries for one seed juniper and pinyon pine. All measurements are in meters.*

Table 1. Discriminant analysis classification for oneseed juniper.

Number of observations	Classified into each zone:				
By sliding window technique	By discriminant analysis 1	2	3	Total	% Correct classifications
1	311	15	0	326	95
2	34	241	52	327	74
3	18	155	1094	1267	86
Total	363	411	1146	1920	
Percentage	18.9	21.4	59.7	100	

quadrats classified in zone 1 by the sliding window technique were placed in zone 2 by the discriminate analysis.

This classification correponds rather closely with the findings of Arnold (1964) in terms of zone location and total number of zones. The only major discrepancy is the addition of a fourth zone by Arnold, which was not detected in this study. Differences in plant composition between the study areas may account for this because not all plant species and plant assemblages necessarily respond in the same fashion to varying biotic and abiotic conditions. Furthermore, Arnold based his classification upon a single juniper; perhaps the differences he noted were not as apparent with all junipers. Lastly, if the transect of this study were carried out farther, possibly another zone could have been defined, i.e., zone 3 may still be under the influence of the juniper.

Zone 1 of the pinyon was located entirely beneath the tree canopy. The edge of this zone was about 1.4 m from the tree bole. Zone 2 was, for the most part, beneath the pinyon canopy, although this was dependent upon direction. The edge of the zone 2, for all directions but west, approximated the canopy edge and was roughly 2.2 m from the tree base (Fig. 2). Zone 3 consisted primarily of interspace. Discriminant analysis results for pinyon pine are shown in Table 2. Zone 3 was the most indistinct because 45 quadrats classified in zone 3 by the sliding window technique should be in zone 1 according to the discriminant analysis.

The outward shifting of the northerly and easterly directions, and corresponding contraction of the southerly and westerly portions of the juniper canopy and the zones themselves are shown in Figure 2. Arnold (1964) also noted a similar effect. We speculate that this is probably the result of increased solar radiation in the south and west directions, and subsequent increased shading in the northerly and easterly directions.

Table 2. Discriminant analysis classification for pinyon pine.

Number of observations	Classified into each zone:				
By sliding window technique	By discriminant analysis 1	2	3	Total	% Correct classifications
1	194	22	15	231	84
2	13	103	22	138	75
3	45	139	374	558	67
Total	252	264	41	927	
Percentage	27.2	28.5	44.3	100	

Zone 1 of the pinyon was only slightly bowed outward in the northerly direction. In the westerly direction, however, the zone boundary extended approximately 0.3 m beyond the canopy edge (Fig. 2). This incongruity is in contrast to the findings of both zone 1 and the results of the juniper analysis. Inadequate sample size and sampling methodology (not sampling each of the 4 cardinal directions for each tree) may have contributed to the suspected error.

Mean basal cover among zones was significantly different for both tree species. Mean basal cover increased from 0.7% in zone 1 to 6.9% in zone 2 to 12.4% in zone 3 around juniper trees (Fig. 3). Mean basal cover increased from 3.7% in zone 1 to 9.9% in zone 2 around pinyon trees. The difference in mean basal cover from zone 2 to zone 3 was nonsignificant ($P>0.05$) (Fig. 3).

The relatively low mean herbaceous basal cover in zones 1 and 2 for both tree species as several possible explanations. Allelopathic effects have been demonstrated by Jameson (1961, 1968) for oneseed juniper and by Lavin (1968), and Jameson (1961, 1968) for pinyon pine. Allelopathic effects and litter acting as a physical barrier to plant establishment have been demonstrated by Schott (1985) and Johnsen (1962) for oneseed juniper, and by Johnsen (1962) for both oneseed juniper and pinyon pine. Severe shading, such as that found beneath the canopy of juniper trees, has a deleterious effect on grasses in terms of vigor (Johnsen 1962) and a

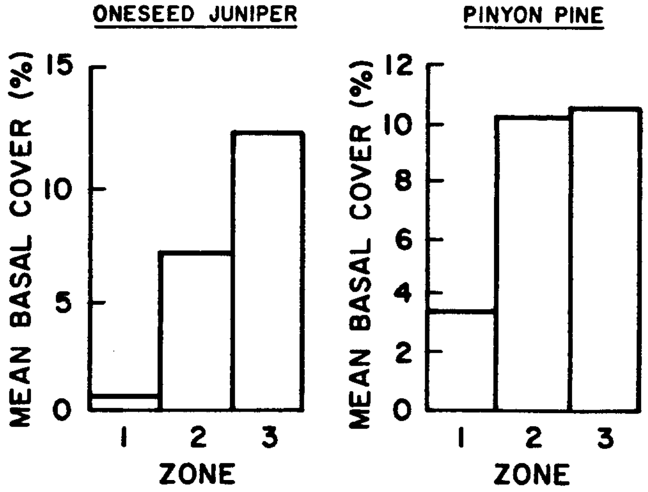

Fig. 3. *Basal cover of herbaceous species in the 3 zones associated with oneseed juniper and pinyon pine.*

basal cover (Schott 1985). Jameson's (1966) finding that pinyon-juniper cover, i.e., shading, did not negatively influence blue grama cover was not confirmed by this study. The juniper canopy also may intercept a significant portion of the total precipitation falling on an area (Gifford 1970, Skau 1964, Johnsen 1962, Young et al. 1984), thereby reducing soil water beneath the tree canopy. Similarly, pinyon pine intercepts light and precipitation, but does not appear to do so to the extent that oneseed juniper does. Presumably, the effects of the tree on understory cover are lessened as the canopy edge was approached and with continuing distance from the tree.

Mean herbaceous basal cover was not significantly different ($P \leq 0.05$) among directions for either the pinyon or the juniper, although mean basal cover was slightly higher in the east and north direction for both species (Table 3). This may result from more mesic conditions in these directions, resulting in less drought stress and higher soil water content.

Table 3. Mean basal cover estimates (%) of each cardinal direction surrounding pinyon pine and oneseed juniper.

Pinyon understory				Juniper understory			
Direction				Direction			
North	South	East	West	North	South	East	West
8.7	8.4	8.0	7.7	6.7	6.6	6.8	6.6

Blue grama and wolftail basal cover varied inversely between the south and north directions for both tree species. Blue grama had its greatest basal cover in the north and its lowest cover in the south. The mean basal cover of wolftail, however, was highest in the south and lowest in the north. Hence, blue grama appears to favor the more mesic directions while wolftail favors the more xeric directions.

Species composition shifts between zones were also apparent for both species (Table 4).

Juniper

Dominant species in zone 1 included blue grama, sand muhly, skunkbush sumac, and algerita. Wolftail, three awns, snakeweed, hairy grama, and sand dropseed were notably absent within this zone. Creeping muhly, scarlet globemallow, galleta, sideoats grama, and blue grama were the predominant species in zone 2. Dominant species in zone 3 included blue grama, galleta, wolftail, mat muhly, scarlet globemallow, three awns, and hairy grama.

Table 4. Mean basal cover estimates (%) of selected species surrounding oneseed juniper and pinyon pine. Means with the same letter are not significantly different ($P \leq 0.05$).

	Pinyon			Juniper		
	1[1]	2[2]	3[3]	1	2	3
Major grasses						
Sideoats grama	0.15a[4]	0.30a	1.0b	0.02a	0.20a	1.1b
Blue grama	2.3a	8.2b	4.6c	0.25a	3.9b	4.4c
Hairy grama	0.00a	0.01a	0.05a	0.00a	0.02a	0.30b
Wolftail	0.11a	0.80b	2.9c	0.0a	0.09a	3.6b
Galleta	0.05a	0.20a	0.60b	0.04a	0.43b	0.50b
Creeping Muhly	0.37a	0.14b	0.01c	0.04a	0.47b	0.01a
Sand dropseed	0.05a	0.08a	0.42b	0.0a	0.18b	0.38c
Major forbs						
Groundcherry sp.	0.09a	0.0b	0.0b	0.03a	0.05b	0.0c
Scarlet globemallow	0.04a	0.06a	0.07a	0.0a	0.21b	0.15c
Half shrub						
Snakeweed	0.03a	0.07a	0.08a	0.0a	0.20b	0.10c
Shrubs						
Algerita	0.02a	0.0a	0.0a	0.05a	0.0b	0.0b
Wolfberry	0.01a	0.0a	0.0a	0.01a	0.0b	0.0b
Skunkbush sumac	0.06a	0.0b	0.0b	0.06a	0.0b	0.0b
Trees						
Oneseed juniper	0.06a	0.0b	0.0b	0.02a	0.0b	0.0b
Pinyon pine	0.02a	0.0b	0.0b	0.02a	0.01b	0.0b

[1] Surrounding the tree bole.
[2] From the tree bole to approximately the canopy edge.
[3] Primarily interspace.
[4] Means with rows with different superscripts are significantly different ($P < .05$) for each tree species.

Pinyon

Dominant species in zone 1 included blue grama and creeping muhly. Species unique to this zone included groundcherry, pinyon pine, oneseed juniper, skunkbush sumac, algerita, and wolfberry. Hairy grama was conspicuously absent within this zone. Predominant species in zone 2 included blue grama, which had its highest basal cover within this zone, sideoats grama, sand muhly, galleta, and wolftail. Dominant species in zone 3 included sideoats, blue grama, galleta, wolftail, sand muhly, and sand dropseed.

These compositional differences may be related to the varying tolerance of different species to the gradients of biotic and abiotic conditions found among zones. Arnold (1964) also noted similar composition changes among zones for oneseed juniper, which were presumably the basis for his zone classification. Everett et al. (1983) also found changes in composition relative to the distance from the tree base and duff boundary in Nevada, although they did not appear to be as distinct as those Arnold (1964) described or the differences found in this study.

Woody species were generally restricted to zone 1 for both tree species. Woody species are probably more prevalent beneath the tree canopy because of concentated avian seed deposition in such locations, although improved microclimatic conditions and reduced competition from grasses may also explain this pattern. Forbs in zone 1 were almost exclusively annuals; they may be related to disturbance, perhaps by small mammal activities beneath the junipers, and either small-mammal or livestock use beneath the canopy of pinyon pine.

These dissimilitudes are probably the result of differences in light and precipitation as related to canopy morphology. Differences in allelopathic toxicity, as well as possible root competition, and differences in animal use patterns may also play a role in these compositional differences.

Knowledge of these vegetational patterns adds to our understanding of the ecology of pinyon-juniper woodlands. In addition, they have implications for the utilization of these areas by livestock and game. Response of herbaceous and shrubby vegetation to manipulation of the tree cover is also influenced by pre-treatment patterns.

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Influence of forest site on total nonstructural carbohydrate levels of pinegrass, elk sedge, and snowberry

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Abstract

Seasonal trends in total nonstructural carbohydrates (TNC) were studied in pinegrass (*Calamagrostis rubescens* Buckl.), elk sedge (*Carex geyeri* Boott), and snowberry (*Symphoricarpos albus* (L.) Blake) in western Montana in 1983 and 1984. Plants were collected from 4 forest sites at approximate 2-week intervals throughout the growing season. The sites were a clearcut and forested area in 2 different habitat types. Total nonstructrual carbohydrates were determined using an enzyme digestion technique and acid hydrolysis. Total nonstructural carbohydrates in pinegrass rhizomes exhibited a U-shaped curve with reduced levels during growth initiation in the spring and increased levels after growth cessation in late summer. Snowberry root crown TNC exhibited a V-shaped curve with rapid drawdown caused by spring growth followed by rapid replenishment of TNC levels. Elk sedge, an evergreen, did not have a stage of development which resulted in large fluctuations in TNC content of roots or root crowns. In general, TNC levels in elk sedge roots and root crowns and snowberry root crowns were greater on forested sites than clearcuts while the opposite was found in pinegrass rhizomes. Phenological development of plants growing under the forest canopy was delayed by 2 to 3 weeks compared to plants growing in the clearcuts. The influence of clipping pinegrass and elk sedge to a 5-cm or 10-cm stubble height in late May and late June was also studied. Elk sedge TNC levels were least affected when plants were clipped to a 10-cm height in late May and most affected when clipped to a 5-cm height in either May or June. Pinegrass rhizome TNC levels were lower than controls 2 weeks after clipping to 5-cm stubble heights in late May and late June, but after 4 weeks TNC levels of 5-cm clipped plants were not different from controls. Clipping to a 10-cm stubble height in late May did not cause a reduction in TNC levels. The 10-cm clipping treatment reduced pinegrass rhizome TNC levels compared to the control 2 weeks after clipping in late June. The replenishment of TNC reserves of elk sedge and pinegrass to moderate foliage removal during the spring suggests that these species may be moderately grazed in early spring when they are more palatable to livestock.

Key Words: *Calamagrostis rubescens, Carex geyeri, Symphoricarpos albus,* transitory range, forest grazing

Forested areas in western Montana provide valuable forage for livestock and wildlife. Production of forage beneath a forest canopy varies among habitat types and as a result of the density and nature of the tree cover (Willard et al. 1983). Clearcutting and other logging methods create transitory range which may provide large quantities of forage for livestock. Pinegrass *(Calamagrostis rubescens* Buckl.), elk sedge (*Carex geyeri* Boott), and snowberry (*Symphoricarpos albus* (L.) Blake) are the dominant forage plants associated with several forest habitat types of the northwest United States and Canada. Pinegrass is a slender, tufted grass that is considered fair forage for cattle and elk (Stubbendieck et al. 1982). Reproduction is by rhizomes or by seed in open areas. Elk sedge is a caespitose, dry land sedge which reproduces by seeds and rhizomes and is considered good forage for cattle and elk (Stubbendieck et al. 1982). Snowberry is a rhizomatous shrub used as browse by cattle, deer, and elk.

Management of forested range is difficult because of the complex of environments which influence forage plant physiology. Also, when logging practices remove the forest overstory, there are changes in precipitation and radiation reaching the soil surface, which influence available soil water, soil temperatures, and forage plant growth and phenology. Trlica (1977) stated there was a need for studies to establish relationships among carbohydrate reserve cycles, growth, and phenological stage of development, and to determine at what phenological stages of development plants are most detrimentally affected by defoliation. Therefore, the primary objective of this study was to describe the seasonal carbohydrate cycles of pinegrass, elk sedge, and snowberry as affected by forest habitat type, canopy cover, and plant phenology. A secondary objective was to determine the influence of clipping on TNC levels of pinegrass and elk sedge.

Study Area

The study sites were located 56 km northeast of Missoula, Montana on the Lubrecht Experimental Forest. The major vegetation types on the forest are second-growth stands of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) or ponderosa pine (*Pinus ponderosa* Laws) with understories consisting primarily of pinegrass, elk sedge, snowberry, and dwarf huckleberry (*Vaccinium caespitosum* Michx.). Annual average temperature on the forest is 4.0° C and yearly precipitation averages 44.3 cm (Steele 1981). January is the coldest month, averaging -8.4° C, while July's 16.8° C average is the warmest. Precipitation is greatest in January and June averaging 6.0 cm and 6.3 cm, respectively. Summer precipitation is low, averaging 2.4 cm in July and 2.7 cm in August.

Four sampling sites representing 2 habitat types each with a clearcut and undisturbed forest area were selected in the spring of 1983. The 4 sampling sites were: (1) a Douglas-fir/snowberry habitat type with a dominant overstory of ponderosa pine, canopy cover averaging 50%, elevation of 1,230 m, 10% slope and southern exposure; (2) a clearcut adjacent to Site 1 with the same elevation, slope and aspect; (3) a Douglas-fir/dwarf huckleberry habitat type with an overstory of Douglas-fir and western larch (*Larix occidentalis* Nutt.), canopy cover averaging 60%, elevation of 1,260 m, slope less than 5%, and northwest exposure; and (4) a clearcut adjacent to Site 3 with the same elevation, slope and aspect. The soil of the ponderosa pine forest and clearcut was a Shooflin silt loam, a member of the very fine, montmorillonitic, Typic Eutroboralfs. The soil of the Douglas-fir forest and clearcut was a Crow silt loam, a member of the fine mixed, Typic Eutroboralfs. The 4 sites will be referred to as the ponderosa pine forest, ponderosa pine clearcut, the Douglas-fir forest, and the Douglas-fir clearcut.

Methods

Sample Collection and TNC Analysis

Elk sedge, pinegrass, and snowberry plants were collected at approximate 2-week intervals from 13 April through 22 October in 1983 and from 19 March through 22 August in 1984. Early summer dormancy occurred in 1984 because of dry conditions and plant collections were terminated. A late fall collection was made on 30

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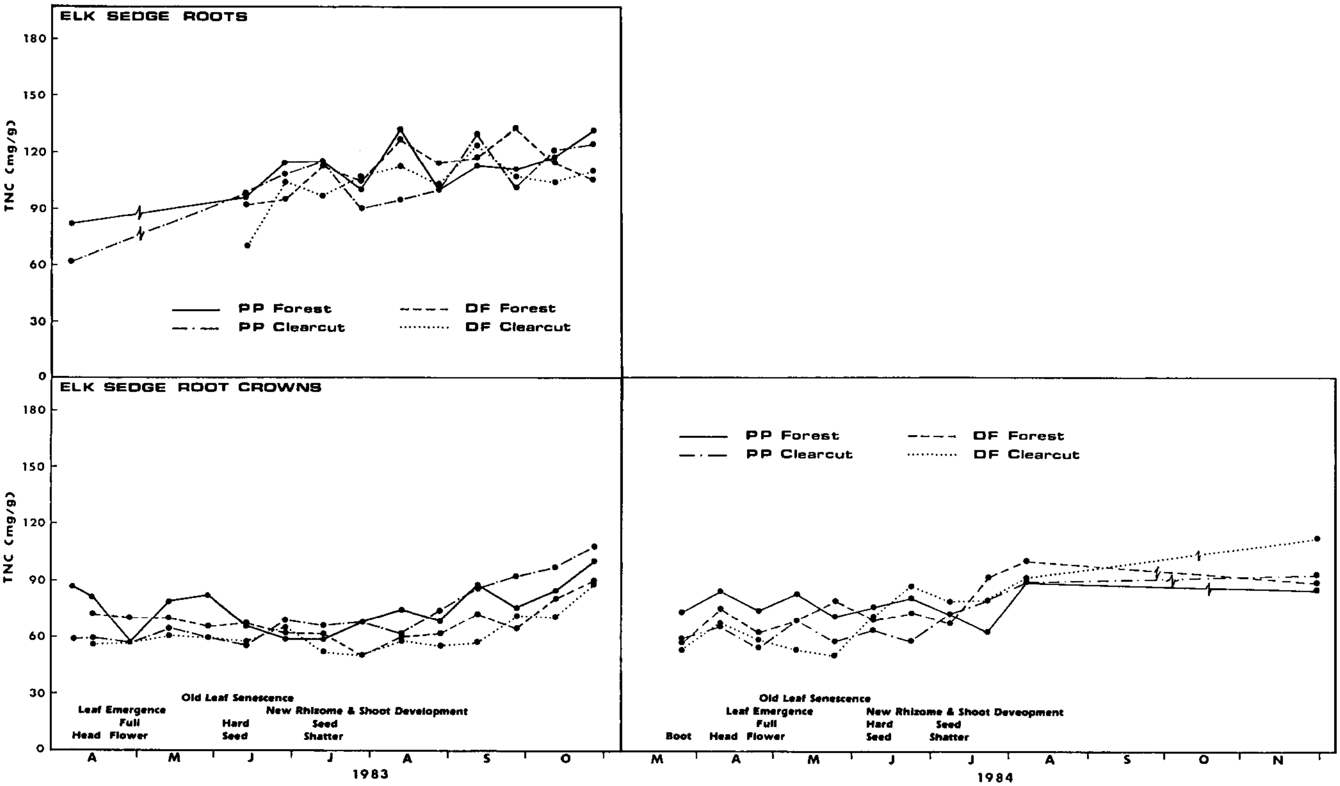

Fig. 1. *The influence of site and date on total nonstructural carbohydrates (mg/g) in elk sedge roots and root crowns in 1983 and 1984. Phenological stages of development are also included.*

November 1984. Five representative plants of each species were collected on each site and date. Sampling began at dawn when air temperatures were low to minimize loss of total nonstructural carbohydrates (TNC) from respiration and to avoid diurnal variation. Stout et al. (1983) reported that TNC levels in combined rhizomes and roots of pinegrass were higher than TNC in root crowns, and the TNC seasonal pattern of crowns was quite erratic. We collected rhizomes to a depth of 20 cm removing all fibrous roots to eliminate their interference. Studies involving the TNC cycles of Nebraska sedge (*Carex nebraskensis* Dewey) (Steele et al. 1984) and *C. lacustris* Willd. (Roseff and Bernard 1979) stress the importance of the TNC content of rhizomes to these species. In elk sedge, rhizomes were often absent or when present usually no more than 1 cm in length; thus, rhizomes constituted only a small portion of the underground tissue. Therefore, we collected all roots to a depth of 20 cm for a belowground sample and a 2-cm to 3-cm section of root crown for an aboveground sample. Crown material of snowberry was defined as the swollen base of the plant located at or below ground level. Crown samples of snowberry included 3-cm of rhizomes from the crown. All samples were immediately placed on dry ice to slow respiration during transport to the lab. The samples were washed with cold water to remove soil particles, dried at 105° C for 10 minutes to stop enzymatic action, then dried at 65° C for 7 days. The dried material was ground in a Wiley mill to pass a 60-mesh screen, then stored in air-tight containers. The phenological stage of development was noted for each plant sampled. Soil temperature was measured at a 15-cm depth on each site and collection date and also at a 30-cm depth on the ponderosa pine sites. Gravimetric soil water (%) was measured using soil cores extracted to 15-cm depth for all sites and all collection dates and also from 15-cm to 30-cm depth on the ponderosa pine sites (Hillel 1971).

Total nonstructural carbohydrate levels were measured in elk sedge and snowberry using an enzyme digestion technique developed by daSilveira et al. (1978). Pinegrass, which is high in fructosans, was treated with 0.4 N H_2SO_4 acid for 20 min after enzyme digestion (Smith et al. 1964). No differences were found in the TNC levels of elk sedge or snowberry tissues before and after acid hydrolysis. TNC concentration in the plant tissue was read spectrophotometrically and expressed on a mg/g dry weight basis (daSilveira et al. 1978).

Clipping Treatments

Moderate and severe clipping treatments were applied to elk sedge and pinegrass on 24 May and again on 23 June 1984 to test for differences in response to early and late herbage removal on the 4 sites. Plants were clipped to a 10-cm stubble height for the moderate treatment or a 5-cm stubble height for a severe treatment (Stout et al. 1980). Four plants of each species of the clipped plants were collected 2 and 4 weeks following clipping to measure the amount of TNC change with time. The amount or regrowth was determined by measuring the length of leaves from the point of clipping at the 2- and 4-week intervals.

Statistical Analysis

The seasonal TNC cycles were compared using a completely randomized design in a factorial arrangement. The factors were site and date with 5 randomly chosen plants per species on each date as replications. We did not replicate the sites, therefore our conclusions about the TNC trends apply only to these sites. The 1983 pinegrass collections were not statistically analyzed because of difficulties in the laboratory. The influence of clipping treatments was determined using a completely randomized design with a factorial arrangement. The factors were treatment (clipping intensity), date, and site. The clipping treatments were replicated (4 replications/treatment) by applying 1 of 3 clipping treatments to randomly chosen plants. When the analysis of variance showed a

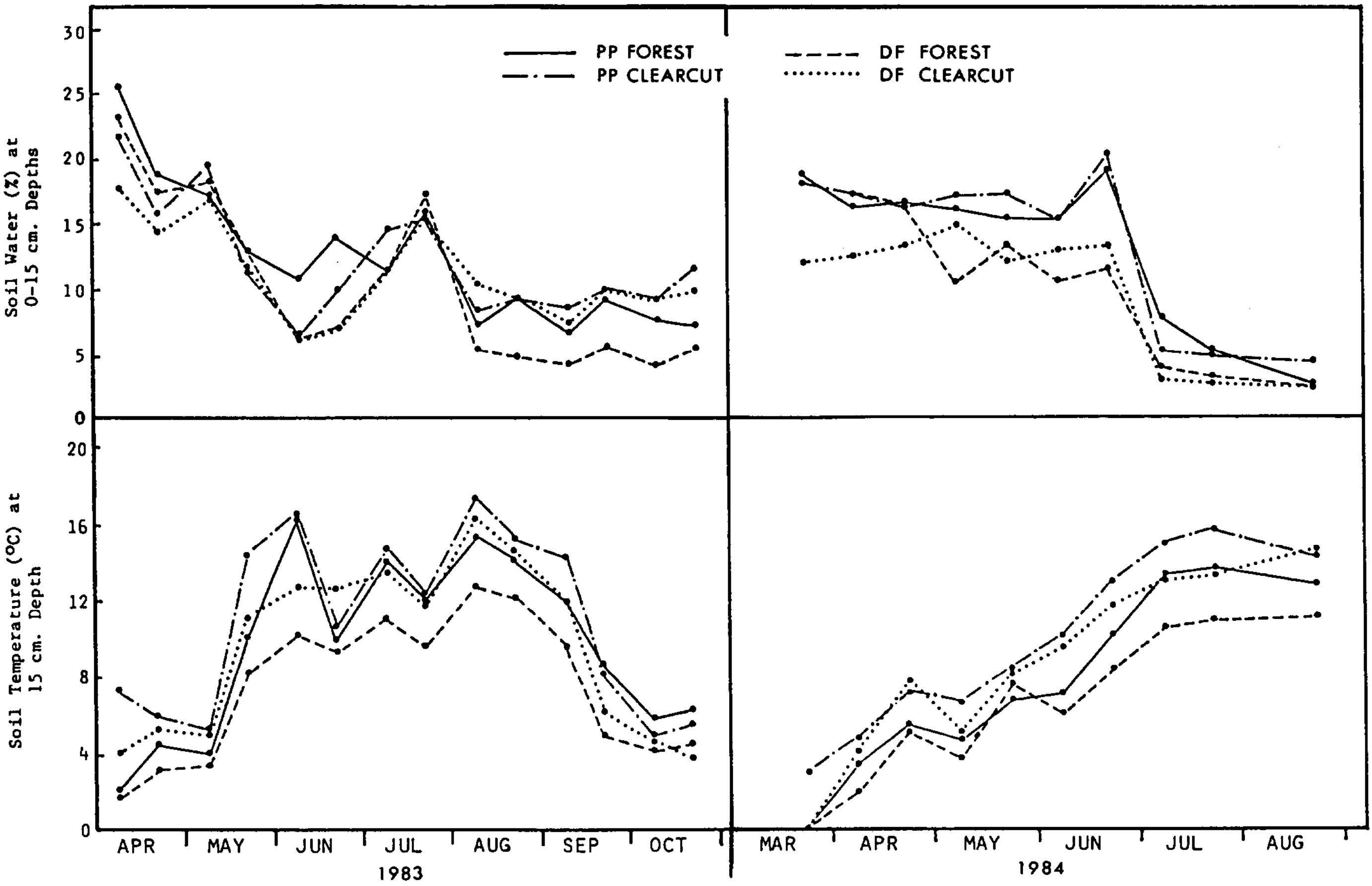

Fig. 2. *Soil water (%) and soil temperature (C) at 15 cm depth by site and date in 1983 and 1984.*

significant treatment effect a Duncan's new multiple range test was used to test all possible comparisons between means (Steel and Torrie 1960). An alpha level of 0.05 was used to test for significant differences.

Results and Discussion

Elk Sedge

The seasonal reserve cycles of roots and root crowns of elk sedge showed little relationship to phenological development (Fig. 1). Root crown TNC levels were lowest in the spring and summer during the periods of leaf emergence, flowering, and seed production. Carbohydrate levels began to increase in late summer as soil water content decreased and soil temperature increased (Fig. 2). Kramer and Kozlowski (1960) reported that seasonal carbohydrate trends vary with different leaf habits; there is less fluctuation in the reserves of evergreen species than in deciduous species because of greater dependence on current photosynthesis than stored food for spring growth. This applies to elk sedge, which remains green over the winter months and retains the previous year's leaves until new leaves are formed the following spring. Late fall TNC levels in the root crowns averaged 96.7 mg/g while early spring levels averaged 60.9 mg/g, indicating that significant amounts of TNC were used for winter respiration.

With all dates combined, TNC levels in elk sedge root crowns were greater in plants growing on the forested sites than on the adjacent clearcuts in 1983 (Table 1). In 1984, TNC levels in roots crowns were greater on the ponderosa pine forest than on the ponderosa pine clearcut; samples from the Douglas-fir forest showed only a trend higher levels than the Douglas-fir clearcut. When the 2 habitat types were compared, TNC was greater in plants on the ponderosa pine sites than the Douglas-fir sites in 1983. There was no difference in TNC levels of roots or root crowns between the 2 habitat types in 1984. Total nonstructural carbohydrate levels in plants are dependent upon the balance between growth, photosynthesis, and respiration and these factors are in turn affected by environmental conditions such as temperature and moisture. Blaser et al. (1966) found that soluble carbohydrates increased in orchardgrass (*Dactylis glomerata* L.) when low temperatures and water stress limited growth. Growth of orchardgrass was reduced relatively more by water stress than by photosynthesis and photosynthesis had a lower optimum temperature than growth. In 1983 and 1984 soil temperatures were lower on the forested sites than the adjacent clearcut sites. Seasonal averages of

Table 1. Total nonstructural carbohydrates (mg/g) averaged over all dates by site and species.

Species and plant part	Site Ponderosa pine forest	 Ponderosa pine clearcut	 Douglas-fir forest	 Douglas-fir clearcut
Elk sedge crowns (1983)	75.4 d[1]	71.5 c	68.8 b	61.8 a
Elk sedge crowns (1984)	77.1 b	67.2 a	75.6 b	70.3 ab
Elk sedge roots (1983)	111.4 b	105.0 a	113.4 b	105.5 a
Pinegrass rhizomes (1984)	71.1 ab	79.4 b	69.2 a	90.4 c
Snowberry crowns (1983)	173.3 c	133.2 a	156.4 b	149.9 b
Snowberry crowns (1984)	174.8 d	132.2 b	156.3 c	112.5 a

[1] Means followed by a similar letter within each row are not significantly different at the 0.05 level of probability.

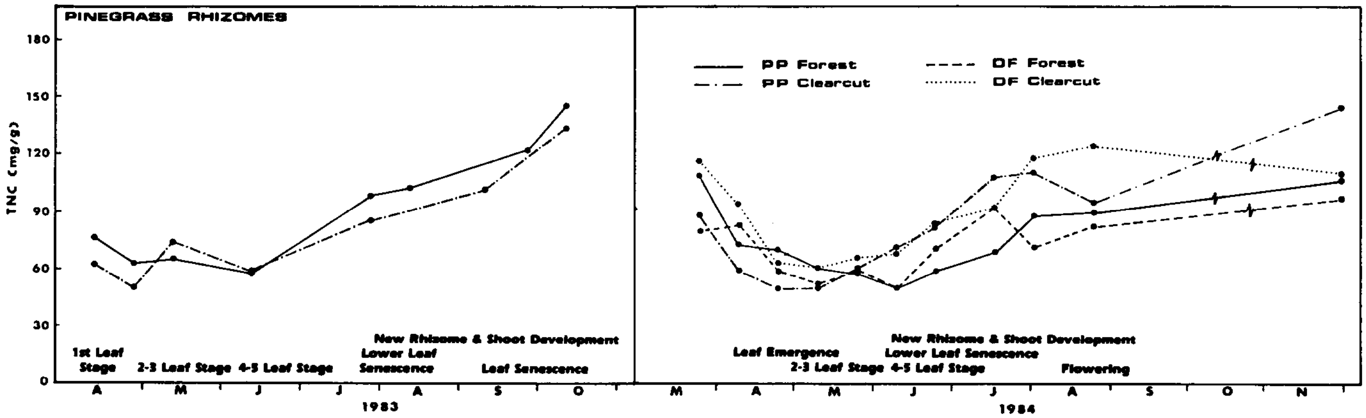

Fig. 3. *The influence of site date on total nonstructural carbohydrates (mg/g) in pinegrass rhizomes in 1983 and 1984. Phenological stages of development are also included.*

soil water content showed no difference among the 4 sites in 1983 or 1984; however, from August through October, 1983, soil water content was significantly less in the forested areas than in the clearcuts (Fig. 2). Vogel (1985) found less soil water in elk sedge rooting zones in a similar forest type compared to elk sedge in an adjacent clearcut. Elk sedge in the forest apparently responded to its environment with reduced growth and higher TNC levels when compared to an adjacent open environment.

Pinegrass

The seasonal TNC cycle of pinegrass can be described as a U-shaped curve (Fig. 3). Growth initiation in the spring caused decreases in TNC content with the lowest levels occurring between the 3rd and 4th leaf stages. Rhizome TNC levels increased in June and July as plants produced new rhizomes and shoots. Descriptions of pinegrass (USDA 1937, Stubbendieck et al. 1982) state that reproduction is primarily by rhizomes except on open sites where flowering sometimes occurs. Only 4 plants were found to produce flowers in the 2 years of collections; thus, it could not be determined whether flowering had an effect on TNC levels.

Total nonstructural carbohydrate levels in pinegrass rhizomes averaged across all dates in 1984 were greater on the Douglas-fir clearcut than the Douglas-fir forest while the 2 ponderosa pine sites were not different (Table 1). Plants on the Douglas-fir clearcut had greater TNC than those on the ponderosa pine clearcut. Although no difference was found between TNC levels on the 2 forested sites, there appears to be a trend toward greater TNC in plants growing on the ponderosa pine forest.

Soil temperatures were significantly higher on the clearcut sites than the forest sites. Vogel (1985) found greater rooting zone soil water content and higher photosynthetic rates of pinegrass plants growing in a clearcut compared to an adjacent forest in a similar site. Therefore, we believe higher photosynthetic rates in pinegrass growing in the clearcut allowed for increased growth and TNC storage compared to pinegrass under the forest canopy.

Snowberry

Snowberry root crowns exhibited a V-shaped seasonal TNC curve with rapid drawdown during early spring growth followed by rapid replenishment (Fig. 4). In 1983 and 1984 the decrease in TNC was much greater in plants growing on the clearcut sites than the adjacent forested sites. The time at which TNC was at its lowest level varied not only by site but also by year. The lowest TNC levels ranged from 22 April on the ponderosa pine forest to 8 June on the Douglas-fir forest. A comparison between 1983 and 1984 showed that the TNC levels were from 3 weeks earlier to 10 days later depending on the site. Flowering of snowberry plants began in June when TNC levels were increasing. Approximately 75% of the plants on the clearcuts flowered compared to less than 20% of the forest plants. Full flower occurred in late July in 1983 and in late June in 1984. Fruit set and leaf senescence also occurred 1 month earlier in 1984 than in 1983. July precipitation was above average in 1983 and below average in 1984. With all dates combined the TNC content of snowberry root crowns in 1983 was greater in the ponderosa pine forest than in the ponderosa pine clearcut, while there was no difference in TNC levels between the 2 Douglas-fir

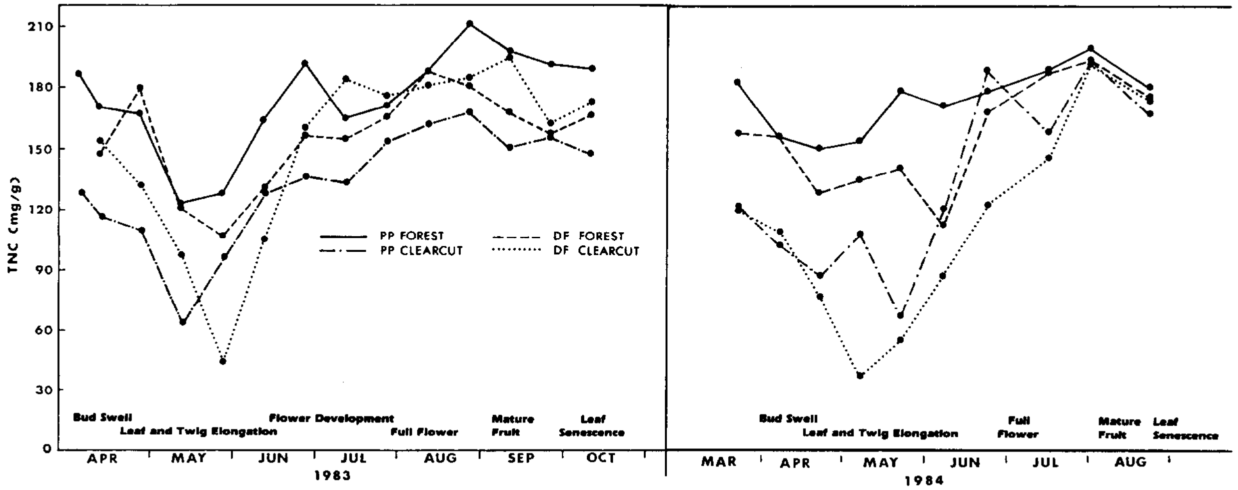

Fig. 4. *The influence of site and date on total nonstructural carbohydrates (mg/g) in snowberry root crowns in 1983 and 1984. Phenological stages of development are also included.*

sites (Table 1). In 1984, snowberry in both the ponderosa pine and Douglas-fir forested areas had higher TNC levels than snowberry in the adjacent clearcuts. Our results indicate that like elk sedge, growth of snowberry is reduced more by water stress than is photosynthesis. Therefore, snowberry growing under a forest canopy with higher water stress and lower soil temperatures have reduced growth and higher TNC levels.

Clipping Treatments

Elk Sedge

Clipping elk sedge plants on 24 May and 23 June caused significant reductions in TNC of root crowns (Table 2). Site differences in root crown TNC for clipped plants were similar to those of the nonclipped plants with the ponderosa pine forest plants having greater TNC levels than the ponderosa pine clearcut plants. There was no difference between the 2 Douglas-fir sites. Response to clipping was similar across all sites, resulting in no significant treatment by site interactions. Root TNC levels in the 10-cm clipping treatment showed no difference between the first clipping date and the second; however, TNC levels in the 5-cm clipping and control were higher after the second clipping date. This difference caused a significant clipping date by treatment interaction.

Table 2. Total nonstructural carbohydrate (TNC) levels in elk sedge root crowns, elk sedge roots and pinegrass rhizomes by clipping date, time following clipping and treatment averaged over all sites.

Elk sedge root crowns

	Clipping Date			
	May 24		June 23	
Treatment	2 weeks[1]	4 weeks	2 weeks	4 weeks
Control	70.8 b (y)[2]	75.8 b (yz)	73.6 b (yz)	79.7 b (z)
10 cm	70.0 b (z)	58.1 a (y)	53.5 a (y)	61.3 a (yz)
5 cm	49.9 a (y)	55.3 a (y)	48.0 a (y)	57.0 a (y)

Elk sedge root

	Clipping Date			
	May 24		June 23	
Treatment	2 weeks	4 weeks	2 weeks	4 weeks
Control	100.7 b (x)	111.5 b (y)	108.3 b (y)	123.1 c (z)
10 cm	97.5 ab (y)	111.2 b (z)	98.7 a (y)	108.6 b (z)
5 cm	89.5 a (y)	96.2 a (y)	95.6 a (y)	99.1 a (y)

Pinegrass rhizomes

	Clipping Date			
	May 24		June 23	
Treatment	2 weeks	4 weeks	2 weeks	4 weeks
Control	59.2 b (x)	73.2 a (y)	90.9 b (z)	97.1 a (z)
10 cm	59.2 b (x)	91.7 b (z)	77.2 a (y)	94.2 a (z)
5 cm	45.9 a (x)	70.3 a (y)	67.2 a (y)	84.9 a (z)

[1] Time since clipping treatment.

[2] Means followed by a similar letter within each column or in parenthesis within each row are not significantly different at the 0.05 level of probability.

Because of the evergreen nature of elk sedge, no phenological stage resulted in large changes in TNC content. However, clipping elk sedge twice before 30 June, during leaf emergence and flowering, caused TNC levels in both roots and root crowns to be reduced 4 weeks post-clipping in the 10- and 5-cm clipping treatments. Average plant regrowth 2-weeks following clipping on 24 May was 5 and 7 cm for the 5- and 10-cm clipping treatments, respectively. Four weeks following clipping on 24 May, average plant regrowth was 13 and 15 cm for the 5- and 10-cm clipping treatments, but only 2 cm regrowth was measured for clipped plants 4 weeks following the 23 June clipping.

Pinegrass

Total nonstructural carbohydrate levels in pinegrass rhizomes were affected by clipping on 24 May and 23 June (Table 2). Site differences were similar to those of the nonclipped plants; the 2 clearcut sites had higher TNC levels than the adjacent forest sites. The 5-cm clipping treatment had lower TNC levels than either the 10-cm treatment or control on all sites except in the ponderosa pine clearcut where the 5-cm and 10-cm treatments were lower than the control. Although there were differences in plant phenology and average TNC levels, response to clipping treatments were similar across all sites resulting in no significant interactions.

Freyman (1970) clipped pinegrass plants to 15-cm stubble heights over 12 different clipping treatments. He found that clipping pinegrass at 2-week intervals throughout the growing season or just before the summer dry period caused reductions in dry matter. Adequate regrowth occurred if clipping was done on or before 30 June, whereas there was no regrowth if clipping occurred after mid-July. Freyman (1970) suggested that the most desirable practice might be to graze pinegrass for 2 weeks in early June and again in August. Stout et al. (1980) found that yield, tiller height, and tiller number of pinegrass were reduced by clipping and that pinegrass was especially sensitive to herbage removal near the time of growth cessation in mid summer. Our study showed that clipping pinegrass plants to 10-cm stubble heights twice before 30 June did not significantly affect rhizome TNC levels 4 weeks after treatment. Clipping to 5-cm stubble heights twice before 30 June caused a reduction in TNC 2 weeks following treatment; however, TNC levels were replenished by 4 weeks. Regrowth for the 5- and 10-cm clipping treatments averaged 16 and 21 cm, respectively, after the 24 May clipping but only 3 and 6 cm after the 23 May treatment. These data support the recommendations of Freyman (1970) and Stout et al. (1980) that pinegrass be grazed early before growth slows down prior to summer dormancy.

Conclusions

Total nonstructural carbohydrates in elk sedge, pinegrass, and snowberry were affected by forest habitat type, forest canopy cover, and date for our study sites. Significant site by date interactions occurred in these species because of differences in plant phenological development and should be considered in formulating grazing practices such as season-of-use and use intensity for forested sites. Each of the species also exhibited different types of TNC curves. Snowberry root crown TNC levels exhibited a V-shaped curve with a large decrease in TNC caused by spring growth followed by rapid replenishment of TNC levels. Because of the evergreen nature of elk sedge, no one phenological stage resulted in large differences in TNC content. However, our clipping study showed that elk sedge TNC levels were reduced when plants were clipped just after flowering and again after seed production in late May and late June, respectively. TNC levels were least affected when plants were clipped to a 10-cm stubble height in late May and most affected when clipped to a 5-cm stubble height in both May and June.

Pinegrass rhizome TNC levels exhibited a V-shaped curve with reduced levels during spring growth and increased TNC levels after growth cessation in late summer. Clipping of pinegrass plants to a 5-cm stubble height in both May and June or clipping to a 10-cm stubble height in late June caused a reduction in TNC levels 2 weeks following treatment; however, after 4 weeks TNC levels were no different than controls. Clipping to a 10-cm stubble height in late May did not cause a reduction in pinegrass rhizome TNC levels. These data support the recommendations of Freyman (1970) and Stout et al. (1980) that pinegrass be grazed early before growth slows down prior to summer dormancy; however, in western Montana we suggest that grazing of most moderate elevation Douglas-fir sites begin by mid-May rather than the first of June.

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Germination responses of desert saltgrass to temperature and osmotic potential

GREG J. CLUFF AND BRUCE A. ROUNDY

Abstract

Desert saltgrass [*Distichlis spicata* var. *stricta* (Torr.) Beetle] is the dominant herbaceous forage on many saline rangelands. The ability to direct-seed this grass would permit revegetaton of disturbed saline soils. Seeding guidelines must be based on an understanding of germination requirements in relation to seedbed conditions. Germination responses to alternating temperatures in relation to sodium chloride (NaCl)-reduced osmotic potentials were studied in the laboratory and seedbed salinity and water potentials were measured in a typical saltgrass stand in Nevada. Optimum conditions for saltgrass germination were at -0.1 MPa osmotic potential and a 20° C differential in cold and warm period temperatures with warm period temperatures above 30° C. Decreasing osmotic potentials from 0 to -2 MPa decreased the rate of germination from 4.5 to 0.3 and total germination from 60 to 9% across all temperature regimes. Water potentials in the lower topographical positions of a typical saltgrass stand after an unusually wet winter were high enough for germination (>-2MPa) in June when temperatures were optimum for germination. In most years and on xeric sites, optimum temperature and moisture conditions would not overlap to result in high germination. Some germination occurs at cooler than optimum temperatures and low osmotic potentials. Some seeds may eventually germinate in saline seedbeds under these conditions but highest germination would be expected when unusually high precipitation or topographic position results in high seedbed water potentials during late spring and early summer when temperatures are optimum. Consequently, irrigation during late spring and summer should produce the best stands of saltgrass from direct seeding. Where irrigation is not possible, saltgrass should be seeded in the fall to permit germination during early spring when temperatures are suboptimum but the seedbed is still moist. Success of nonirrigated seedings will be highly dependent on seedbed salinity and moisture conditions in the spring.

Key Words: salinity, plant establishment, range revegetation, seedbed ecology

Desert saltgrass is an important forage species of many inland salt marshes of the western United States (Nielson 1956). Saltgrass is not considered to be as palatable as many other endemic grasses; however, it is relatively high in protein (Hanson et al. 1976), is grazing tolerant, and may provide the only available forage for cattle during the summer portion of the grazing season. Because it is salt tolerant and rhizomatous, saltgrass is considered a potential candidate for revegetation of mine spoils and roadsides (Butler et al. 1973, Pavlicek et al. 1977). Revegetation using saltgrass rhizomes is labor intensive, requires specialized equipment, and has limited success (Pavlicek et al. 1977, Caplan 1983). Revegetation by direct seeding could be more effective than planting rhizomes. An understanding of seed requirements for germination in relation to natural seedbed conditions is important in determining seeding constraints and guidelines.

In a previous study (Cluff et al. 1983), desert saltgrass seeds did not germinate at osmotic potentials as low as those measured during the growing season in saturated soils from 2 typical saltgrass stands in Nevada. It was hypothesized that germination and seedling establishment were episodic events, occurring only during seasons of higher than normal precipitation when enough salt could be leached from the soil to raise the osmotic potential to within the limits necessary for germination. This osmotic potential limit is around -1.5 MPa when the seeds are incubated for 1 month at an optimum temperature regime for germination. That temperature regime consisted of 16 hours at 5° C and 8 hours at 40° C. This temperature regime occurred in June or July in the seedbeds of 2 saltgrass stands in the cold desert in Nevada. Since the probability of receiving substantial precipitation during those months is very low (Houghton et al. 1975), optimum seedbed temperatures for germination would rarely overlap with high enough soil osmotic potentials for germination in more saline seedbeds.

Another hypothesis which could explain the germination of saltgrass in saline seedbeds is that seeds may germinate very slowly at cold temperatures in March and April. Suboptimum temperatures may affect the rate of germination more than the total germination. Numerous studies with different plant species have shown that low osmotic potentials may inhibit germination less at suboptimum than at optimum temperatures (Springfield 1966, Odegbaro and Smith 1969, Francois and Goodin 1972, and Sharma 1976). Eventually, some saltgrass seeds may germinate at suboptimum temperatures and low osmotic potentials.

The purpose of this study was to determine the long-term germination responses of desert saltgrass seeds under different temperature regimes to reduced osmotic potentials and interpret these responses with respect to seedbed conditions.

Methods

In October 1981, pistillate seedheads of desert saltgrass were collected by hand from a salt marsh area in the Stillwater National Wildlife Refuge, Churchill County, Nevada. The saltgrass at the site inhabits a 20 M-wide zone between an intermittent fresh-water lake and surrounding silt-dunes which are sparsely covered by greasewood [*Sarcobatus vermiculatus* (Hook.) Torr.] The seeds were cleaned using an air-screen and stored in the laboratory at room temperature at low humidity.

Experimental procedures of Young et al. (1968) were used to determine the interactive effects of osmotic potential and temperature on saltgrass seed germination. Polyurethane foam was placed in polystyrene boxes, 11 by 11 by 4 cm in dimension, with moisture-tight lids and saturated with sodium chloride solutions with osmotic potentials of 0, -0.1, -0.5, -1.0, -1.5, and -2.0 MPa (Lang 1967). NaCl was used as the osmotic agent because it has been shown that it is not toxic to germinating saltgrass seeds (Cluff et al. 1983), produces relatively stable osmotic potentials in widely fluctuating temperatures, is easier to handle than other osmotic agents (Young et al. (1983), and is one of the dominant salts on western rangeland soils (Roundy 1984). Because the seeds were being tested in alternating temperatures and the osmotic potential of any solution varies slightly with temperature, the solutions were made for the means of the fluctuating temperature regime. In no cases did the actual osmotic potential differ by more than -0.05 MPa from the stated potential. Four replications of 25 seeds each were placed on top of the foam in each box. Replications were separated

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by placing them inside circles made from 2.5 cm length of 4.4 cm diameter polyvinyl chloride pipe. The seeds were incubated in dark germinators for 2 months, and germination counted every 2 to 3 days. In pilot experiments, seed germination did not respond to various light treatments. Seeds were considered germinated when the radicle had emerged at least 2 mm. The seeds were tested at 28 cool/warm period temperature regimes including 0/20, 25, 30, 35, 40, 45, and 50° C; 2 and 5/25, 30, 35, 40, 45, and 50° C; 10/30, 35, 40, 45, and 50° C; 20/40, 45, and 50° C; and 30/50° C. Seeds were exposed 8 hours to the cool temperatures and 16 hours to the warm temperatures in each 24-hour period. These temperature regimes were used because they were the only regimes that could be tested in standard germinators, which resulted in germination significantly higher (p=0.05) than zero in the previous study (Cluff et al. 1983). The seeds were tested at each of 6 osmotic potentials in each of the 28 temperature regimes. Since the experiment was conducted over a period of 1 year, germination was tested at the beginning and end of the experiment. Germination was tested after the method of Young and Evans (1979) using 4 replications of 25 seeds each placed on germination paper in petri dishes and kept moist with tap water. The seeds were incubated in dark germinators for 4 weeks at the temperature regime that was found to be optimum for germination in the previous study (Cluff et al. 1983): 16 hours at 5° C and 8 hours at 40° C.

The rate of germination was calculated for each temperature regime-osmotic potential treatment after Maguire (1962) where:

$$\text{Rate of Germination} = \Sigma_i[g_i - g_{(i-1)}/i]$$

in which g is the total germination percentage on an incubation day i minus the total germination percentage on the previous day $g_{(i-1)}$ divided by the incubation day i.

A response surface (Evans et al. 1982) using linear, quadratic, and interaction terms for cold and warm temperatures and osmotic potential was fit to germination percentage and rate data. Optimum temperature regimes were considered those for which mean germination responses at zero MPa osmotic potential were statistically similar (p>0.05) to that of the temperature regime with the highest germination responses. Suboptimum temperature regimes were those with significantly lower germination than maximum caused by what was believed to be a low warm period temperature. Slopes and intercepts of the regression of germination percentage and rate on osmotic potential were compared for optimum and suboptimum temperature regimes (Snedecor and Cochran 1971).

To relate germination responses to seedbed conditions, seedbed salinity and water potential of the saltgrass stand where seeds were collected were determined from samples collected on March and June 30, 1983. Seedbed temperatures would be expected to be suboptimum and optimum for germination at these dates, respectively. Samples were collected from 5 topographic positions with increasing distance from an intermittent fresh-water lake. The positions were edge of standing water, middle and edge of the marsh basin and saltgrass stand, and slopes and tops of adjacent upland silt dunes (Young et al. 1986). The top 3 cm of soil was sampled with a 2 cm-diameter auger at 4 locations for each topographic position and placed in a water-tight bottle. Approximately 2 g of the soil in each bottle were placed in psychrometer chambers described by Brown and Collins (1980). Total water potential of the samples was measured at 25° C before and after saturation with distilled water. The electrical conductivity of the saturated paste extract (ECe) of each sample was determined using methods and equipment described by Roundy (1984). An instant salinity meter was used to measure the electrical conductivity of the saturated paste (ECp) which was converted to the ECe using a linear regression of ECe on ECp calculated from 30 samples.

Results

There was no change in the germinability of saltgrass seeds over the 1-year period of testing. Seeds tested at the beginning and end of the experiment averaged 84 and 88% germination, respectively.

Percent and rate of germination decreased with increasing cold period temperature, decreasing warm period temperature, and decreasing osmotic potential (Figs. 1 and 2). Maximum percent and rate of germination was at the 0/40° C regime at each osmotic potential. No germination occurred unless there was at least a 20° C difference between cold and warm period temperatures.

Although there was a large reduction in percent germination as osmotic potential decreased, some seeds still germinated at -2 MPa

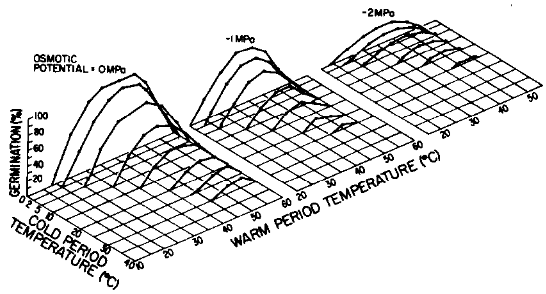

Fig. 1. *Quadratic response surface estimates of percent germination of desert saltgrass as a function of cold and warm period temperatures at 0, -1 and -2 MPa osmotic potential. The coefficient of determination (R²) for the response surface was 0.75.*

Table 1. Unsaturated and saturated soil water potential and saturation extract electrical conductivity (ECe) in the upper 3 cm of a saltgrass stand at Stillwater, Nevada in 1983.

	Topographic Position				
Sample date	Edge of lake	Middle of lake basin and saltgrass stand	Edge of lake basin and saltgrass stand	Slopes of silt dunes	Top of silt dunes
			ECe (dS m^{-1})		
March 20	0.7b[1]	2.5b	8.3b	19.6a	7.1a
June 30	2.6a	54.4a	85.9a	10.8b	11.4a
			Actual soil water potential (MPa)		
March 20	−1.05a	−0.67a	−0.95a	−5.55a	−6.23a
June 30	−0.43a	−1.59b	−7.0b	−7.0b	−7.0b
			Saturated soil water potential (MPa)		
March 20	−0.63a	−0.43a	−0.48a	−2.05b	−1.38b
June 30	−0.36a	−1.34a	−4.36b	−0.63a	0.66a

[1] Comparisons are made between dates for a given variable and topographic position. Means for dates followed by the same letter are not significantly different (p=0.05).

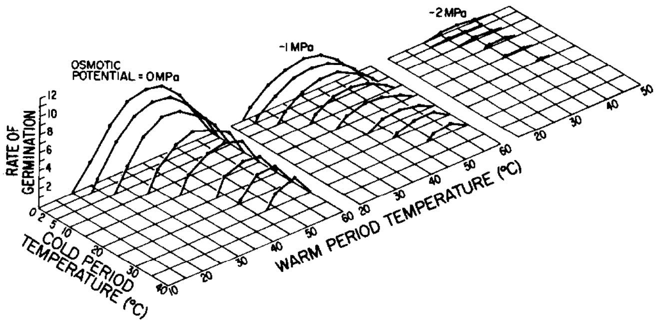

Fig. 2. *Quadratic response surface estimates of rate of germination of desert saltgrass as a function of cold and warm period temperatures at 0, -1 and -2 MPa osmotic potential. The coefficient of determination (R^2) for the response surface was 0.59.*

osmotic potential. The average reduction in total germination was from 60% at 0 MPa to 9% at -2 MPa osmotic potential. Percent germination was not reduced from 0 to -0.1 MPa. The rate of germination was reduced from 4.5 at 0 MPa to 0.3 at -2 MPa osmotic potential.

Optimum temperature regimes with average germination percentages and rates not significantly different from maximum were 0/35, 0/40, 0/45, and 2/40° C. Suboptimum regimes with lower germination responses than maximum were 0/25, 2/25, 5/25, and 5/30° C. These regimes all had at least a 20° C cold-warm period temperature differential, so reduced germination was considered to be due to suboptimum warm period temperatures.

As osmotic potential decreased, percent and rate of germination were reduced more at optimum than suboptimum temperature regimes (Fig. 3). The slope of percent and rate of germination as a function of osmotic potential (-MPa) was significantly lower for suboptimum than optimum temperature regimes (-16.7 and -41.7; -1.1 and -4.2, respectively for percent and rate of germination).

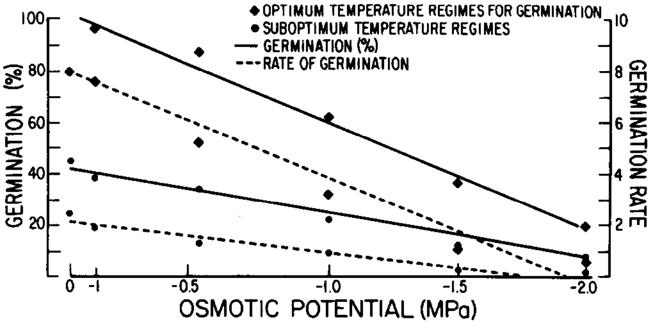

Fig. 3. *Linear regressions of percent and rate of germination of desert saltgrass seed on osmotic potential at optimal and suboptimal temperature regimes for germination. Simple correlation coefficients (R^2) were 0.97 and 0.73 for percent germination at optimum and suboptimum temperatures, and were 0.93 and 0.70 for rate of germination at optimum and suboptimum temperatures, respectively.*

In a typical saltgrass stand, seedbed salinity and water potential varied with season and topographic position (Table 1). Generally, salinity increased and soil water potential decreased with distance and increasing elevation from standing water at the edge of the lake to the silt dunes above the lake basin. Water potential was lowest at the tops of the dunes where saltgrass was absent and highest in the middle of the stand and the edge of the lake where saltgrass was very dense. Salinity was highest at the margin of the saltgrass stand and, at the end of June, in the middle of the stand.

Salinity increased and soil water potential decreased from March to June. Soil water potentials at the edge of the saltgrass stand decreased from potentials high enough for germination to potentials far too low for germination. Soil water potentials were not significantly lower at the end of June than in March in the middle of the saltgrass stand even though salinity was higher. This was probably because the middle of the lake basin and saltgrass stand was flooded by runoff water by the end of June. At the end of June, soil water potentials averaged -1.5 MPa in the middle of the saltgrass stand. Winter precipitation for this area during the sampling year (1983) was 190% of normal (U.S. Department of Commerce 1983).

Discussion

Optimum conditions for germination of saltgrass are high water potentials and a 20° C differential in cold and warm period temperatures with warm period temperatures above 30 but less than 60° C (Cluff et al. 1983). These temperature-moisture conditions would rarely occur in saline seedbeds in the cold desert of the western United States. Surface soil water potentials decrease rapidly in the spring in the salt desert as temperatures increase and soil water from winter or spring storms evaporates (Roundy et al. 1984). Optimum temperatures for saltgrass germination occurred from May through the summer in 2 saltgrass stands measured by Cluff et al. (1983). One of these stands was that where seeds were collected and salinity and water potentials were measured in this study. In 1980, water potentials of the seedbed of this stand were never greater than -2 MPa when temperatures were optimum for germination. However, in 1983, unusually high winter precipitation resulted in flooding of the stand and high enough water potentials for germination in lower topographic positions of the stand when temperatures were optimum in June. High germination of saltgrass could occur when topographic position or weather conditions result in high seedbed water potentials in late spring and summer. Seeds in moist areas such as near the edge of a marsh or lake or depressions where water collects could have high germination. We have observed natural germination of saltgrass seeds in the summer on the beach of Pyramid Lake in the salt desert in western Nevada. Natural saltgrass stands are most dense on these moist sites and the grass apparently spreads onto more xeric or saline sites by rhizomes. High germination on xeric sites would only be expected during years of unusually high and frequent spring and summer precipitation. Due to the possibility of poor seedling survival, it may be nonadaptive for saltgrass or other halophytes to have high germination at low osmotic potentials (Roundy 1987). Chapman (1974) suggested that natural leaching of surface salts may be necessary for halophyte germination in saline soils.

The present study confirms the possibility of another way that saltgrass seeds may germinate in saline seedbeds. Some germination occurs after long incubation periods at optimum and suboptimum temperatures and low osmotic potentials. A percentage of seeds in the seed bank could eventually germinate when day and night temperatures differ by 20° C and water potentials are at least greater than -2 MPa. These conditions and saltgrass germination would most likely occur on less saline but more xeric sites in early spring and on more saline but move mesic sites in spring and early summer. Other possible mechanisms for germination of saltgrass and other halophyte seeds might be by natural stratification or osmoconditioning (Young and Evans 1981). Osmoconditioning is the soaking of seeds at controlled osmotic potentials and temperatures to allow germination processes to begin but not to allow radical emergence (Koller and Hadas 1982). Increased rate, percentage, and uniformity of germination and seedling growth are reported responses to artificial osmoconditioning (Khan et al. 1980/81). Moist, saline seedbeds in winter may naturally stratify or osmocondition saltgrass or other halophyte seeds resulting in rapid germination when temperatures increase in spring. The biological responses to natural stratification and osmoconditioning and their ecological significance in the establishment of halophytes are important subjects for future research (Roundy 1987).

The above observations suggest some recommendations for revegetation by direct seeding with saltgrass. In areas without dependable summer rain, best stands of saltgrass will be obtained by irrigation in the spring and summer when seedbed temperatures are optimum. Where irrigation is not possible, fall seeding should result in emergence of some saltgrass during early spring when temperatures are suboptimum for germination but seedbeds are still moist. The success of such nonirrigated seedings will be highly dependent on soil salinity and spring moisture conditions.

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Use of leader lengths and diameters to estimate production and utilization of *Cercocarpus breviflorus*

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Abstract

Weight relations for twig lengths and diameters were determined for hairy mountain mahogany plants in southern New Mexico. Both twig lengths and twig diameters were related linearly to twig weights. Twig length and twig diameters explained more than 80% of the variation in twig weight. The equation $\hat{y}(g) = -0.68 + 0.3$ (length) + 6.33 (diameter) resulted in the highest r^2 (0.88) value compared to either length or diameter alone. Thus, twig length and diameter measurements could be used to determined production and utilization of hairy mountain mahogany. These relationships probably, however, vary with environmental context.

Key Words: hairy mountain mahogany, twig length diameter relationships

Estimating current production and utilization of shrubby species poses difficult problems for those managing shrub ranges. Shrubs are often large plants which are difficult to harvest. They frequently exhibit indeterminant growth during the current season which is often difficult to distinguish from that produced during previous growing seasons. Consequently, techniques other than clipping have been developed for determining production and utilization of important browse species.

One approach has been to work with individual branches or leaders of the shrub. In this case, twig length and diameter have been related to twig weight (Telfer 1969, Lyon 1970, Ferguson and Marsden 1977, and Provenza and Urness 1981). The procedure involves determining the relationship between length or diameter and twig weight. Production can then be estimated from length or diameter measurements alone. Individual twig weights would need to be multiplied by twig numbers for entire shrubs to express biomass on an area basis.

Length: diameter and weight:diameter ratios offer considerable

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Table 1. Regression equations for best models predicting leader weight for hairy mountain mahogany.

Equation	r^2	Standard Error			
		Intercept	Slope	Length	Diameter
$\hat{y}$ (grams) = $-.08 + 10.03$ (diameter)	0.85	0.005	.381	—	—
$\hat{y}$ (grams) = $-0.32 + 0.08$ (length)	0.80	0.004	0.003	—	—
$\hat{y}$ (grams) = $-0.68 + 0.03$ (length) + 6.33 (diameter)	0.88	0.052	—	0.005	0.681

promise for estimating utilization solely from post-browsing measurements. Diameter measurements after browsing provide estimates of total twig length and weight before browsing. The remaining portion of the twig can be clipped and weighed, its length and percentage utilization easily computed (Basile and Hutchings 1966). It may also be possible to estimate utilization by measuring diameter of the twig at the point where it was browsed and estimating the weight of that portion removed. Measurement of diameter at that point of attachment would allow one to estimate the weight of the intact twig.

The objective of this study was to determine length:weight and diameter:weight relations of hairy mountain mahogany (*Cercocarpus breviflorus* [Gray] Wright), one of the most important browse species in New Mexico.

Description of Area

The study site was located in the Organ Mountains Recreation Lands in Dona Ana County, approximately 45 km northeast of Las Cruces, New Mexico. The study area consisted of approximately 20 ha immediately north of the Bureau of Land Management picnic site. The elevation of the area ranges between 1,219 and 2,743 m at Organ Peak.

The climate of the region is characterized by mild winters, hot summers, and dry, windy springs. Most winter moisture is a result of low-intensity rains or occasionally snow. Summer precipitation occurs as a result of convectional thunderstorms of high intensity (Paulsen and Ares 1962). The majority of the annual rainfall (55% of the average annual precipitation) is received during the period from July through September (Herbel et al. 1974).

There are no available climatic data for the Organ Mountain Recreation Lands. Generally, it can be assumed that higher elevations receive more moisture and have less extreme summer temperatures, while winter temperatures are more extreme and solar radiation is more intense than on areas at lower elevations (Moir 1963).

Vegetation of the study area was described by Moir (1963). Tall hairy mountain mahogany shrubs dominate the area, constituting approximately 44% of the shrub composition. The canopy varies from dense to widely spaced. On more favorable drainages or less exposed areas, *Quercus grisea* Liebm. and *Garrya wrightii* Torr. prevail. The understory small shrub species include *Yucca baccata* (Engelm.) Tre., *Nolina microcarpa* Wats., *Agave* sp., *Rhus trilobata* Nutt., and *Fallugia paradoxa* (D. Don) Endl. Typical species under conditions of rockiness and thin soil mantle are *Mimosa* sp., *Opuntia* spp., *Applopappus* sp., and *Dasylirion wheeleri* Wats. The vegetation is clearly shrub-dominated and grass species never form pure stands.

Methods

In November 1980, 126 leaders representative of the current year's growth were randomly selected from 20 individual plants located on both north and south aspects and hand-clipped. They were clipped at the point of attachment to the stem and air-dried for 2 weeks. Measurements of twig length and diameter were recorded. Lengths were measured to the nearest 0.1 cm. Diameters were measured to the nearest 0.01 cm at 1 cm, 3 cm and 5 cm from the base of the twig using a vernier caliper. Leaves were then separated from leaders and weighed to the nearest 0.001 g. There were no significant differences ($P<0.05$) in leader length, diameters or weight from plants on north and south exposures. Consequently, data were combined for the regression analysis.

Leader diameter-length-weight relations were established through all possible regression analysis (Draper and Smith 1966). Leader weight was the dependent variable. Leader length, diameters at 1, 3 and 5 cm, and percent leaf weight were the independent variables. They were used individually and in all possible combinations. Another set of equations was developed through transformation to logarithmic form.

Results

Regression equations relating air-dry leader diameters at 1, 3, and 5 cm from the base, leader length, and percent leaf weight to leader dry weight were established from samples of 126 leaders. Diameters 5 cm from the base for samples ranged from 0.8 to 2.6 mm. Length ranged from 5.5 to 25.7 cm and weight ranged from 0.13 to 2.34 g. A simple linear regression equation providing the best description of data was in the general form $\hat{y} = B_o + B_1x$. The highest single predictor ($r^2 = 0.85$) of leader weight was leader diameter measured 5 cm from the base. The regression equation obtained was $\hat{y} = -0.8 + 10.03x$ (Table 1). Logarithmic transformation of data improved predictive power slightly ($r^2 = 0.87$). A lower coefficient of determination ($r^2 = 0.80$) was obtained when leader length was used instead of leader diameter as an independent variable and the regression equation was $\hat{y} = +0.32 + 0.08x$ (Table 1).

Discussion

Higher correlation of weight with diameter than length for mountain mahogany was in agreement with data of Provenza and Urness (1981) for blackbrush (*Coleogyne ramosissima* Torr.), Lyon (1970) for serviceberry (*Amelanchier alnifolia* Nutt.), Basile and Hutchings (1966), and Ferguson and Marsden (1977) for bitterbrush (*Purshia tridentata* [Pursh.] D.C.).

Several authors have emphasized the effect of site, years, browsing pressure, overstory canopy, and years on these twig weight-diameter-length relationships (Basile and Hutchings 1966, Ferguson and Marsden 1977, Halls and Harlow 1971, Lyon 1970, Peek 1971, and Rutherford 1979). From these studies, we should be warned that frequent checks may be necessary to assure application of the most appropriate equation. For instance, data from bitterbrush plants in southeastern and southwestern Idaho revealed similar y intercepts, but rather large differences in regression coefficients (Basile and Hutchings 1966, Ferguson and Marsden (1977). In other cases, general equations may apply across a wide array of conditions (Bartolome and Kosco 1982, Provenza and Urness 1981). Because we sampled at only the one date, it is not possible to know how general our results are.

The leader diameter-weight regression equation yielded higher accuracy and predictability than the length-weight equation for hairy mountain mahogany. However, leader lengths were easier to measure in the field than diameters.

Use of these procedures for utilization estimates rests on the assumption that leaves are not eaten independently of leaders (Ruyle et al. 1983, Smith and Urness 1962). Leaves contributed from 23 to 70% of total leader weight of hairy mountain mahogany in this study. If browsing animals strip leaves off, then these methods would not be appropriate, unless leaves were accounted for (Ruyle et al. 1983).

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Analysis of Russian thistle (*Salsola* species) selections for factors affecting forage nutritional value

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Abstract

The need for forage plants that are productive in, and adapted to, semiarid conditions prompted us to examine the range and independence of assortment of nutritional qualities of wild stands of Russian thistle (*Salsola* species). Seventy selections from a 5-state area of the southwestern United States were planted in observational plots and analyzed for crude protein, acid detergent fiber, lignin, nitrate, water-soluble oxalate, in vitro digestibility, and ash content at 2 stages of maturity. Values on a dry matter basis of crude protein (5.4 to 22.3%), acid detergent fiber (20.1 to 48.8%), acid detergent lignin (3.1 to 10.4%), nitrate (0.1 to 5.1%), water-soluble oxalate (0.2 to 9.1%), plant height (40 to 180 cm at second harvest), stage of development (midbloom to complete seed development at second harvest), and degree of prickliness (soft to extremely prickly at second harvest) were determined for each of the 70 selections at 2 harvest times. The color, branch density, and degree of leafiness were examined at the second harvest only. Values for in vitro digestibility (45.1 to 66.3% organic matter disappearance) and ash (12.7 to 30.5% of dry wt) were determined for a subset of 22 samples. About 10% of the selections had a composite of properties which would suggest they they would make moderate to good forages.

Key Words: crude protein, in vitro digestibility, acid detergent fiber and lignin, nitrate, water soluble oxalates

Plants of the annual, ruderal forb *Salsola iberica* (or *S. pestifer* or *S. kali,* see Beatley 1973) and related species can provide forage for grazing cattle for 8 months out of the year on southern New Mexico ranges (Nelson et al. 1970), and are considered fair to excellent forages on western range lands (Esplin et al. 1937, Cook et al. 1954, Nelson et al. 1970). During periods of drought, Russian thistle (*Salsola* species) hay has provided major sustenance for cattle in the western United States. For example, farmers in western Kansas harvested 400,000 tons of Russian thistle in 1934 for silage and hay (Cave et al. 1936). Potential nutritive value of Russian thistle plants for preparing hay or silage has been recognized for some time (Bailey and Gustafson 1902, Cave et al. 1936, Donaldson and Goering 1940), and its use in preparing standard diets for farm animals has been described (Harris et al. 1968). More recently, its nutritional potential was confirmed with plants grown under controlled conditions in the greenhouse (Farmer et al. 1976) and under cultivation in the field (Fowler and Hageman 1978, Hageman et al. 1978). Little effort has been expended in the United States to improve rangelands by deliberately introducing selected plants of the genus *Salsola,* but work has been done in the Soviet Union to promote the growth of several species including *Salsola orientalis* (Abdraimov 1981). Worldwide importance of making more efficient use of arid and semiarid lands for food production by introducing and improving new plant species has been discussed by a number of authors (McKell 1975, Upchurch 1981, Hinman 1984).

To achieve our long-range goal of domesticating *Salsola* for use as a forage, it was essential to know whether positive and negative nutritional factors assort independently in plant populations already established in the desert Southwest. No systematic studies have been done to assess the range of potential nutritive values, or

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potentially toxic components such as nitrate or oxalate, of the 3 species of Russian thistle (*S. iberica, S. paulsenii,* and *S. collina*) described by Beatley (1973), and introgrades thereof, in spite of the fact that these are widely distributed and grazed by livestock in the semiarid southwestern United States.

We describe here physical, chemical, and biological properties of plants from 70 selections of *Salsola* species gathered over a 5-state area and grown under uniform, irrigated field conditions. Results suggest considerable genotypic and phenotypic variation exists within these populations, and positive and negative characteristics of nutritional significance assort independently. Thus, it should be possible to obtain improved forage species of *Salsola* by traditional selection and breeding methods. Several selections had composites of properties which should make them good forage plants, whereas many more of the selections would be predicted to be fair to poor forages.

Materials and Methods

Seeds of 514 individual plant selections were collected from mature *Salsola* plants from 5 western states (Arizona, California, Nevada, New Mexico, and Texas) between November 1983 and March 1984. Plants with a wide range of phenotypic variability, and from a large number of different environmental sites were selected. Seeds were harvested by cutting a single plant at its base and threshing it by hand on a large aluminum pan (1 m^2). Seeds and debris were stored in paper bags until they were cleaned using a Clipper seed cleaner. Cleaned seeds were stored at 22° C until planted. Seeds were planted at the Leyendecker Plant Science Research Center (14 km south of Las Cruces, New Mexico). The soil, Armijo clay loam (fine montmorillonitic, thermic Typic Torrent), was disked, leveled, fertilized (with 224 kg/ha of 18-46-0), listed in 76-cm rows, and irrigated. When suitably dry, beds were mulched and later harrowed to flatten the tops of rows, cultipacked, irrigated with a sprinkler system to soften clods and firm bed tops and, once dry on top, were again cultipacked to provide a firm, well-pulverized seedbed.

The 514 selections of *Salsola* seeds were planted at a depth of 2 cm and covered by the press wheel only using John Deere 71 Flexiplanters fitted with cone seeders. Seeds were planted at a rate of 5 g/7.6 m of row in observation plots with 324 of the selections planted in 2-row plots of 7.6 m and 190 of the selections (in cases where seed was limited) in single-row plots. Alleys of 1.5 m separated the ends of the rows. After planting, the field (0.63 ha) was irrigated 3 times for stand establishment (25, 26, and 28 May 1984) using a sprinkler system. Plots were further irrigated on 29 June by sprinkler with 4.1 cm of water. Most of the water for plant maintenance, however, came from rainfall (15.9 cm).

Seventy selections representing a cross-section of phenotypes among the 514 original selections were chosen for more detailed study. Physical characteristics of plant height, stage of maturity, degree of prickliness, canopy color, relative canopy density, and relative degree of leafiness were determined. Chemical analyses of crude protein, acid detergent fiber (ADF), acid detergent lignin (ADL), nitrate, and water soluble oxalates were made on 2 harvests. Samples representing a range of protein content, 22 of the 70 selections, were chosen for in vitro digestibility analyses. Plants were harvested at 50 and 118 days after planting (DAP) by cutting a 0.5-m section of plants (10–20 plants) from the center of a row at a height of about 10 cm from the ground. Plants were immediately dried in a forced-draft oven at 65° C until constant weight was reached. Partially dried material was passed through a large Wiley mill fitted with a 6-mm mesh screen. A thoroughly mixed 50–100-g subsample was ground in a small Wiley mill fitted with a 40-mesh screen and stored in screw-capped glass jars. Total dry matter was determined by drying duplicate 1-g portions of the ground subsamples at 110° C for 24 h according to the method of Harris (1970); the water content of partially dried samples averaged less than 4%. All values reported here for chemical analyses were calculated on a 100% dry-weight basis.

Crude Protein

A slightly modified version of the AOAC micro-Kjeldahl method (AOAC 1980, p. 858) was used for crude protein determinations. Samples (0.200 g) were digested using circa 0.5 g of Kelpac Powder No. 2 (Curtin Matheson Scientific) and 4 ml of concentrated H_2SO_4. Twenty ml of deionized H_20 were added after digestion to dissolve solids. For distillation, a few grains of Zn dust and 20 ml of 50% NaOH were added. Distillate (30 ml) was collected in a 2.9% boric acid solution containing methyl purple indicator, and titrated to the end point with 0.1 N HCl. All assays were done in duplicate or triplicate.

Acid Detergent Fiber and Lignin

The AOAC method (AOAC 1980; p. 134-135) was used, except that Hyflo Super-Cel (Fisher Scientific) replaced asbestos for the crucible mats. All assays were done in duplicate or triplicate using 1-g samples.

Nitrate

The procedure of Cataldo et al. (1975) was followed without modification. All samples were analyzed in duplicate and the results expressed as percent NO_3^-.

Oxalates

The AOAC method (AOAC 1980, p. 541-542) was modified slightly using procedures outlined by Baker (1952) to accommodate a dried plant sample, rather than a canned vegetable product, and to allow for the determination of water-soluble as well as total (soluble and insoluble) oxalates. Insoluble oxalates are not toxic to animals because they are not absorbed, but excreted without effect (Kingbury 1964). Oxalates were determined on duplicate subsamples by titration with 0.01 N $KMn0_4$. Results are expressed as percent oxalate as oxalic acid.

Mineral Ash Analyses

The AOAC method (AOAC 1980, p. 125) was slightly modified for the ashing of samples. Duplicate 1-g samples were ashed in aluminum weighing pans for 4.5 to 5 h at a temperature of 500 to 600° C in a muffle furnace to achieve complete ashing of samples. A few samples were ashed in fritted glass crucibles rather than aluminum weighing pans for comparison purposes. No differences were seen in the results obtained by the 2 methods.

In Vitro Dry Matter and Organic Matter Disappearance

The in vitro digestibility analyses were performed in triplicate using the method of Tilley and Terry (1963), with slight modifications, by staff in the NMSU Animal Science Nutrition Lab. The following modifications were made. A 0.5-g sample was suspended in a total volume of 35 ml (4:1, McDouglas solution:rumen fluid). After flushing with CO_2, the vessels were covered with a perforated cap and acid pepsin digestions were stopped by freezing. Samples were filtered through Whatman No. 541 paper.

Phenotypic Measurements and Characteristics

Plant height, stage of maturity, and degree of prickliness at each harvest date were determined. Plant height was measured in centimeters from the top of the bed to the uppermost part of the plant in several locations within the plot, and the mean value was recorded. The stage of maturity was determined on the basis of flowering with plants grouped into 5 stages: prebloom—no apparent flowers; early bloom—flowers just beginning to show; midbloom—approximately half of the plant in flower; late bloom—plants fully covered with flowers and seed beginning to set; and mature—most seed fully developed. Degree of prickliness was determined by touch. The prickliness of *S. iberica* is caused by a single needle-like spine on the tip of each leaf and floral bract.

Results and Discussion

The ultimate goal of the research described here is to select and

Table 1. Mean values and ranges of physical and chemical factors useful in predicting forage value in 70 field-grown *Salsola* plant selections at 2 harvest dates.[1]

	Harvest 1 50 days after planting		Harvest 2 118 days after planting	
Physical/chemical factor	Mean ± S.D.[2]	Range	Mean ± S.D.	Range
Plant height (cm)	57 ± 12	30 - 75	113 ± 32	40 - 180
Crude protein[3]	14.4 ± 3.5	9.2 - 22.5	10.4 ± 3.0	5.4 - 17.5
Acid detergent fiber[3]	27.4 ± 3.0	20.1 - 34.2	34.7 ± 5.2	26.5 - 48.8
Acid detergent lignin[3]	4.3 ± 0.6	3.1 - 6.1	6.8 ± 1.2	4.7 - 10.4
Nitrate[3]	0.76 ± 1.2	0.1 - 6.2	0.4 ± 0.4	0.1 - 1.8
Water soluble oxalates[3]	4.4 ± 1.2	1.9 - 9.1	1.9 ± 0.8	0.2 - 4.1

[1] Complete descriptions and values for individual *Salsola* selections are available from the authors upon request.
[2] S.D.-standard deviation of the sample mean.
[3] Percent dry weight.

breed varieties of *Salsola* which can be cultivated as forage crops or used to improve range forage in semiarid regions.

Observations on 70 *Salsola* selections (of the total of 514 planted) revealed that selections varied from each other in height (Table 1), color (reddish-brown, red, yellow green, green and blue-green), prickliness (intensely prickly to soft at 118 days after planting), canopy density (very dense to open), leafiness (very high ratios of leaf-to-stem to low ratios) and time to maturity (less than 50 to more than 118 days after planting). Although several of the physical properties are of obvious importance with regard to forage value, the most important observation made was that within a given selection the plants were remarkably uniform with respect to these physical descriptors (and often strikingly different for plants of selections in neighboring rows). Thus, it should be possible to isolate and breed a *Salsola* variety with a readily recognizable set of phenotypic characters. In addition, some of these descriptors may correlate with nutritionally important factors. For example, none of the selections which had a reddish color was found to have a high protein content (all 14% or less).

The highest crude protein values were generally found in younger plants and, as a rule, decreased as plants matured. In 10 selections, crude protein content did not change, or increased slightly, during the period examined; however, this property did not appear to correlate in any obvious way with other physical characters. At 50 days after planting (DAP), 17 selections had crude protein content as high as that typical of alfalfa at first cutting in Dona Ana County, New Mexico (18.8±0.9%). In most cases, but not all (3 exceptions), high crude protein levels were associated with high nitrate content.

The quality of the protein found in plants at 50 DAP was examined by carrying out amino acid analysis on acid hydrolyzates of 9 selections, representing plants with crude protein contents of 9.6–20.4%. Although proline, tryptophan, and methionine were not determined in this study, the average values of all other amino acids showed little variation from one plant selection to another, were nutritionally well-balanced, and were essentially the same (data not shown) as values previously reported (Hageman et al. 1978).

The acid detergent fiber content, in contrast to protein, tended to increase as the plants matured, but 4 exceptions to this trend were seen. Acid detergent fiber content of plant selections harvested at the same time were fairly uniform, varying by only a factor of 1.7 at both 50 and 118 DAP. One remarkable selection had about 49% acid detergent fiber at 118 DAP; the same selection was low in nitrate, oxalate, and protein but was highly prickly. Another selection was also high in fiber, low in nitrate, oxalate, and protein, but retained a soft and leafy character until 118 DAP. Thus, certain desirable and undesirable characters appear to assort independently.

Of all characters examined, nitrate content was the one that varied most dramatically. At 50 DAP, selections examined varied from 0.1 to 6.2% nitrate (more than 60 fold). Forty-seven selections had nitrate levels below 0.45%, even at early stages of growth, which would be considered quite safe in a forage (Crawford et al. 1961, Murphy and Smith 1967, and references therein). In fact, cattle have been reported to graze, without ill effects, on forages containing an average of 2% nitrate (Heath et al. 1985). As with protein content, we found that nitrate levels generally decreased, often sharply, as plants matured, which is consistent with reports on other forages used for livestock grazing (Crawford et al. 1961). Six selections did have nitrate levels (2.4–6.1% at 50 days after planting) that might be toxic. Since 3 of the selections examined had high crude protein content, but only moderate or relatively low nitrate levels, protein and nitrate content might be selected independently.

Water soluble oxalates varied in these samples (Table 1), but without exception older plants had less oxalate than younger plants. At 50 DAP, several strains contained oxalic acid levels that might be toxic to sheep (in the absence of calcium supplements), but by 118 DAP, nearly all strains contained levels of oxalate (<3%) that would be safe even for sheep (Davis 1973).

No consistent level of toxicity for oxalates has been established in ruminants. We measured soluble oxalate levels in *Salsola*

Table 2. Mean values and ranges of ash content and in vitro digestibility indicators of 22 selections of *Salsola* at 2 harvest dates.[1]

	Harvest 1 50 days after planting[2]		Harvest 2 118 days after planting[3]	
Digestibility indicators	Mean ± S.D.[4]	Range	Mean ± S.D.	Range
Ash content	24.2 ± 2.9	21.3 - 30.5	15.8 ± 2.0	12.7 - 20.7
DMD[5]	68.5 ± 2.1	64.7 - 72.1	59.6 ± 4.4	51.6 - 67.7
OMD[6]	62.1 ± 2.2	58.9 - 66.3	53.7 ± 4.8	45.1 - 62.8

[1] Values for individual *Salsola* selections are available from the authors upon request.
[2] Average protein and acid detergent fiber for samples from Harvest 1 are 14.9 and 21.7%, respectively.
[3] Average protein and acid detergent fiber for samples from Harvest 2 are 11.0 and 34.6%, respectively.
[4] S.D.–standard deviation of the sample mean.
[5] DMD–percent dry matter disappearance.
[6] OMD–percent organic matter disappearance.

Table 3. Correlation coefficients among forage nutritive properties of *Salsola*.

	CP	ADF	ADL	NITRATE	OXALATE	ASH	DMD	OMD
DAY	–0.51**	0.72**	0.80**	–0.21**	–0.77**	–0.81**	–0.68**	–0.64**
CP		–0.78**	–0.65**	0.66**	0.73**	0.74**	0.52**	0.52**
ADF			0.85**	–0.43**	–0.77*	–0.86**	–0.76**	–0.77**
ADL				–0.32**	–0.78**	–0.77**	–0.77**	–0.73**
NITRATE					0.42**	0.57**	0.19*	0.20*
OXALATE						0.88**	0.67**	0.64**
ASH							0.80**	0.78**
DMD								0.99**

*,**Significant at 5% and 1% levels, respectively.

because of reports from Australia of its toxic effect on sheep grazing on drought-stressed *Salsola kali* (Mathams and Sutherland 1952); however, no reports of oxalate toxicity in cattle grazing *Salsola* have appeared. James et al. (1975) claimed plants with levels of soluble oxalate under 10% are not toxic to ruminants, and Heath et al. (1985) have pointed out that rumen bacteria can efficiently degrade oxalate. Oxalate toxicosis and tolerance in ruminants has been reviewed recently (Smith 1986).

In vitro digestibility (Table 2) compared favorably with the range seen for alfalfa hay (53 to 70.4%), and was generally higher than that reported for grasses (Norris et al. 1976, Heath et al. 1985). Earlier work on range samples has shown calcium levels in *Salsola* plants were high compared to those of most grazed species, and phosphorus levels were adequate for cattle (Nelson et al. 1970).

Pearson correlation coefficients were determined for a number of the components analyzed in this study (Table 3). Most values are similar to those expected for typical forages. Weak correlations between oxalate and nitrate suggest these characters are assorting independently. Interestingly, both oxalate and ash displayed fairly strong positive correlations with organic matter disappearance. We believe this may be accounted for, in part, by the presence of digestible calcium oxalate, which declines with maturity.

In summary, we have shown that selections of wild stands of *Salsola* grown under uniform field conditions have a wide degree of phenotypic expression of characters potentially important for forage production and that positive and negative factors can assort independently. In addition, 7 of the current 70 selections which were analyzed appeared to be suitable for cultivation as forages, or for introduction in range situations, because desirable factors were moderate to good and the undesirable traits were low. Further selection, breeding, and analysis will be required to test the reproducibility of these properties. As Davis (1973) stressed in an analogous study of *Astralagus* (milkvetch) species, other factors in addition to the ones measured here may be important in determining which plants might make the greatest improvement in range forage value.

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Using the Green and Ampt infiltration equation on native and plowed rangeland soils

NEIL C. HUTTEN AND GERALD F. GIFFORD

Abstract

Soil textural relationships were used on 3 soil series on both plowed and native rangeland to predict Green and Ampt infiltration equation parameters. Infiltration rates predicted from the Green and Ampt soil texture relationships were regressed against field infiltration rates. Good predictability was found on only 4 of 94 plots, all of which were in the agricultural area. Results indicate that current soil texture relationships developed for estimating infiltration rates may not be sufficient for use in either agricultural or rangeland semiarid environments. At this point in time, if infiltration values are important, then they should be measured (not estimated) using appropriate methodologies.

Key Words: Green and Ampt, infiltration, soil texture, rangeland soils

Minimal research has been directed at predicting infiltration rates on western rangelands. Several examples of a multiple regression approach to predicting infiltration are available, but the equations are site specific, vary with season and among years, and some of the independent variables may be more difficult to measure than infiltration itself (Gifford and Busby 1974, Williams et al. 1972, Gifford and Skau 1967, Meeuwig 1970, Blackburn 1975, Busby and Gifford 1981, Bedunah and Sosebee 1985).

McCuen et al. (1981) have suggested that soil texture data can be used to predict Green and Ampt infiltration equation parameters on agricultural lands. The rate form of the Green and Ampt (1911) equation is:

$$f = K(1+nS/F) \tag{1}$$

where f = infiltration rate (cm/hr), K = hydraulic conductivity in the wetted zone (cm/hr), n = available porosity (%), S = suction parameter (cm), and F = cumulative infiltration (cm). The equation assumes a homogeneous soil with uniform moisture content; a negligible depth of water ponded on the surface throughout the calculation; that each plot acts as a point; and that the entire plot is contributing when runoff begins. Devaurs and Gifford (1986) were generally unsuccessful in their attempts to use soil textural relationships to predict Green and Ampt equation parameters on 3 rangeland sites on the Reynolds Creek Experimental Watershed near Boise, Idaho. The objective of this study was to determine the applicability of using rangeland soil properties on plowed and native rangeland soils to predict parameters in the Green and Ampt infiltration equation.

Methods

Study Area

During summer of 1983, 96 rainfall simulator plots were randomly located on various soil series on both agricultural land (converted from rangeland) and native rangeland in northern Utah. There were 2 sampling periods, from 9 June to 7 July, ("early"), and from 23 August to 15 September ("late") (Table 1). The following measurements were taken on each plot during both sampling periods:

1) Infiltration over a 30-minute period in 2- to 5-minute increments (cm/hr)
2) Soil bulk density (2.5 and 7.6 cm depths)
3) Particle size distribution (soil textural class) (2.5 and 7.6 cm depths)
4) Organic matter content (2.5 and 7.6 cm depths)
5) Antecedent soil moisture (7.6 cm depth)

Table 1. Distribution of rainfall simulator plots with soil series during each of two sampling periods.

No. plots per sampling period	Soil series with classification
	Plowed Area
8	Kearl loam 4–15% slopes
	A coarse—loamy, mixed, frigid Calcic Haploxeroll
8	Jebo very gravelly loam 25–40% slopes
	A loamy—skeletal, mixed, frigid Calcic Haploxeroll
8	Gobine silt loam 1–10% slopes
	A fine—silty, mixed, frigid Typic Calcixeroll
Native Area	
8	Kearl loam 4–15% slopes
8	Jebo very gravelly loam 25–40% slopes
8	Gobine silt loam 1–10% slopes

The climate of the area is continental and is influenced by the local topography (Campbell and Lacey 1982). It is characterized by low humidity, generally low precipitation on the valley bottom, and wide ranges in temperature. Most of the precipitation in winter falls as snow and is associated with Pacific storm fronts that move across the northern part of Utah from the west. Summer precipitation consists mainly of infrequent but often intense convective thunderstorms. Normal annual precipitation of the study area is about 44 cm. Temperatures range from −17° C in January to 27° C in July. Average length of freeze-free season at the study area is about 90 days. Total pan evaporation at nearby Laketown for the months May to October is 92 cm.

Vegetation in the native area consists of sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* spp.), mule ear (*Wyethia* spp.), arrowleaf balsamroot (*Balsamorhiza sagittata)*, and associated grasses and forbs. Range condition, though not determined, would probably be classified no higher than fair. In the agricultural area, vegetation consists chiefly of winter wheat with some invading forbs.

Land use in the area consisted of cattle grazing prior to plowing (1981), and continued as grazing in the native area. A majority of the study area is included in a 2,021-hectare grazing lease administered by the Utah Division of State Lands. This lease allows for grazing up to 344 animal unit months (Richard Wilcox 1984 personal communication). Actual numbers of livestock on the area at any given time are not available, however.

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Field Procedures

Infiltration rates were determined with a modular drop-forming rainfall simulator as described by Chow and Harbough (1965) and modified by Meeuwig (1971) and by Malekuti and Gifford (1978).

Runoff plots were established by driving steel frames (61 × 61 cm) into the soil (about 7.6 cm). The soil within the plots was prewet by applying 6.4 cm of water 12 to 16 hours prior to rainfall simulation and covered to prevent evaporation.

The simulator was calibrated to produce 7.6 cm/hour rainfall intensity throughout a 30-minute run. During the first 10 minutes of rainfall, runoff samples were taken at 2-minute intervals; thereafter, samples were taken at 5-minute intervals. Based on data from Laws (1941), the kinetic energy associated with this simulator, when run at a height of 183 cm, is about 40% of that of natural rainfall.

Average drop size was 2.8 mm. Water was obtained from a nearby state park and was potable. Infiltration, as defined here, is rainfall minus runoff and includes water absorbed into the soil, water intercepted by vegetation, and water held in depressions and in transit across the plot surface at the moment runoff was sampled.

Surface soil characteristics were sampled following each infiltrometer run. Two samples of surface material (core diameter, 7.6 cm; core depth, 2.5 cm and 7.6 cm) were taken to determine bulk density (g/cc); particle size distribution was determined by the hydrometer method (Bouyoucos 1962) and soil organic matter was determined by colorimetric analysis (Sims and Haby 1971).

Average antecedent soil moisture was measured by randomly locating an additional plot frame adjacent to the 8 runoff plots on each soil series and prewetting it in the manner described above. Two soil samples were taken from this plot during the day the rainfall simulator was operated. One sample, taken in the morning was used to determine soil moisture in those runoff plots operated in the morning. The second sample taken in the afternoon represented soil moisture in the runoff plots operated in the afternoon.

Soil pits were excavated to 61 cm adjacent to each set of 8 plots within each map unit in both the native and agricultural areas. Soil pedon descriptions were made at each point to determine whether the site selected was indeed within the named soil series or within an inclusion. In no case did the pedon descriptions differ appreciably from those in the soil survey report of Rich County (Campbell and Lacey 1982) for the soil series indicated in Table 1.

The Green and Ampt infiltration equation (equation #1) was fitted to f versus 1/F pairs for each infiltration run by least squares regression. The fitted curve was then used to determine the time to ponding. Using the standard equation of a line $Y = mX + b$ where m = slope and b = intercept, if $Y = f$ and $X = 1/F$, the slope is KnS and the intercept is K. Separate values for n and S cannot be obtained.

The field-obtained soil texture, bulk density (both 7.6 cm and 2.5 cm depths), antecedent moisture data and organic matter content (7.6 cm depth) were used to predict Green and Ampt equation parameters using procedures outlined in Brakensiek et al. (1982), and modified by Brakensiek and Rawls (1984). Exponential equations which describe the texture triangles were used to obtain the Green and Ampt suction parameters, S, and the saturated hydraulic conductivity, Ks (Brakensiek, personal communication). The available porosity, n, was calculated as the effective porosity, ϕ_e, (from exponential formulas), minus the antecedent soil moisture. The antecedent soil moisture was obtained from field data as described above. The total porosity, ϕ, was determined from field-obtained bulk density data, assuming a soil particle density of 2.65 g/cc. The effective porosity, ϕ_e, was calculated as total porosity, ϕ, minus residual soil water, ϕ_r (from exponential formulas). The K used by Brakensiek in the Green-Ampt equation is equal to one-half the saturated hydraulic conductivity ($K = Ks/2$) as found by Bouwer, in Brooks and Corey (1964). Using the K and n S thus obtained, the integrated form of the Green and Ampt infiltration equation is

$$F - nS(\ln(1 + F/nS)) = Kt \qquad (2)$$

where t = time (hrs), was solved for F (using Newton's method) at the time intervals used in the field.

Infiltration rates predicted from the Green and Ampt soil texture relationships were regressed against infiltration rates determined in the field. A 1:1 correspondence of texture predicted rates with field-observed rates and a zero y intercept would indicate perfect predictability. T-tests were used to test whether y intercepts were equal to zero, and slopes were equal to 1.

In determining infiltration rates by the soil texture predictors, the time scale was adjusted so preponding was initialized at the start of the rainfall. Delta T (ΔT), the time correction, is equal to TP, the time to ponding, minus TA, the equivalent time for the preponding infiltration if it had occurred with ponding conditions. The term TA was determined as follows (Hawkins, personal communication):

$$TA = ((1/K * (FP - nS * (\ln(1+FP/nS)))) \qquad (3)$$

where: FP = infiltrated volume at time of ponding

$$= \frac{nSK}{i - K}$$

i = rainfall application rate (cm/hr)
other terms are defined previously.

Results and Discussion

Of 94 plots tested in early and late 1983 (data from 2 plots were unsatisfactory), only 4 plots (4%) had intercepts equal to zero ($\alpha = 0.05$) and slopes equal to 1 ($\alpha = 0.05$). Of the remaining 90 plots, some had slopes equal to 1 but intercepts did not equal to zero. Others had slopes not equal to 1 but had intercepts equal to zero. Still other plots had both slopes significantly different from 1 and y intercepts significantly different from zero (Table 2).

The results from 2 representative plots are shown in Figures 1 and 2. In all cases, texture-predicted 30-minute infiltration rates were less than 30-minute rates observed in the field. Generally, the Green and Ampt texture-predicted parameters best fit the data

Table 2. Results of comparisons of texture predicted infiltration rates with field observed rates.

Early 1983
- Plowed Soils, n = 23
  - 4 plots (17.4%) had slopes equal to one.
  - 4 plots (17.4%) had y intercepts equal to zero.
  - no plots had both slope equal to one and y intercept equal to zero.
- Natve Soils, n = 23
  - 8 plots (35%) had slopes equal to one
  - 1 plot (4%) had y intercepts equal to zero.
  - no plots had both slope equal to one and y intercept equal to zero.

Late 1983
- Plowed Soils, n = 24
  - 11 plots (46%) had slopes equal to one
  - 12 plots (50%) had y intercepts equal to zero
  - 4 plots (17%) had both slope equal to one and y intercept equal to zero.
- Native Soils, n = 24
  - 8 plots (33%) had slopes equal to one
  - 2 plots (8.3%) had y intercepts equal to zero.
  - no plots had both slope equal to one and y intercept equal to zero.

Overall n = 94
- 4 plots (4%) had both slope equal to one and y intercept equal to zero.

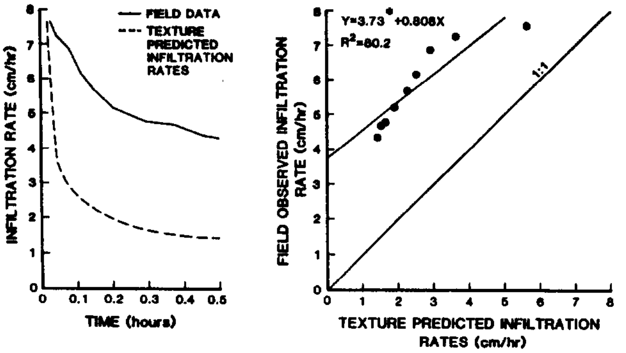

Fig. 1. *Comparisons of field measured infiltration rates and texture predicted rates of 1 field plot of Kearl loam, agricultural area, early 1983. A) Field observed and texture predicted rates versus time. B) Field observed rates versus texture predicted rates. A star (*) indicates the intercept is significantly different from zero (= 0.05). Slope equals 1. Each point represents a specific time interval.*

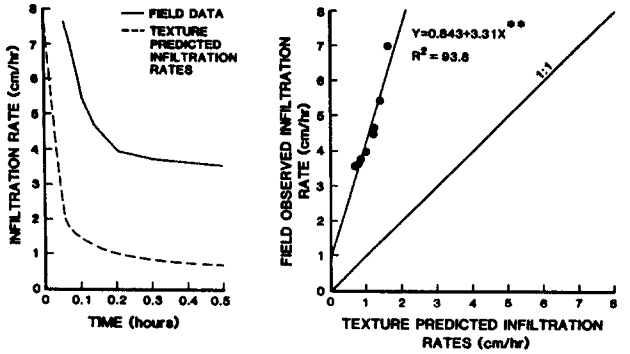

Fig. 2. *Comparisons of field measured infiltration rates and texture predicted rates of 1 field plot of Kearl loam, native area, early 1983. A) Field observed and texture predicted rates versus time. B) Field observed rates versus texture predicted rates. Two stars (**) indicates the slope different from 1 (= 0.05). Intercept equals zero. Each point represents a specific time interval.*

when the infiltration rate on a given plot was low and exhibited rapid drawdown. There was usually a 1 to 4 cm/hour discrepancy between the field rates and the soil-texture predicted rates during the 12 to 30-minute time interval (0.2–0.5 hr).

The soil-texture prediction method developed for agricultural soils needs to be revised before it is suitable for use on agricultural and rangeland settings in semiarid environments. First, surface roughness and recency of plowing (or other treatment) may have a significant impact on infiltration rates (something which currently is not being considered). Second, soil porosities in this study area (and possibly others) may be higher than on sites from where the soil texture relationships were developed. Third, the role of vegetal cover and slope is not considered.

Hutten and Gifford (1988) utilized multiple regression analyses to determine important rangeland plot characteristics that affect infiltration rates on this site. Simple linear regressions on a single soil series frequently resulted in high R^2 values for a single predictor variable. However, no single plot characteristic correlated consistently with infiltration rates or erosion for all soil series. Indeed, set of predictors with the best fit often changed from the 10- to the 20- and from the 20- to the 30-minute infiltration rates. Furthermore, relationships between rangeland soil properties, vegetal cover, and hydrologic response change with soil series as well as season. Previous studies (Blackburn 1975, Devaurs and Gifford 1984, Gifford and Busby 1974, and Williams et al. 1972) have found similar results.

Brakensiek et al. (1982) have attempted to predict infiltration rates using bulk density, soil texture, and organic matter as the sole predictors. It is not surprising that this methodology was not successful in the present study. There are complex interrelationships between the above variables and other rangeland variables such as percent vegetal or litter cover, rooting habits, surface roughness, etc. In the long run it may be easier and more accurate to measure infiltration rates in rangeland environments than to estimate them.

Summary

Field conditions differ from the assumptions used in deriving the Green and Ampt infiltration equation. These underlying assumptions include a homogeneous soil with uniform moisture content, a negligible depth of water ponded on the surface throughout the calculation, that each plot acts as a point, and that when runoff begins the entire plot is contributing. The Green and Ampt infiltration equation also does not explicitly consider vegetation, land condition, or spatial variability. Under the field conditions in this study, all of these assumptions were not met. However, the study reported here was prompted by the current interest in the application of the Green and Ampt equation to rangeland infiltration rates.

Results indicate that Green and Ampt parameters predicted from soil texture data do not adequately reflect rangeland infiltration rates. Ninety-four plots, evenly divided between native and agricultural sites and between early and late 1983 sampling periods, were used in an attempt to validate the soil-texture predictive method for Green-Ampt parameters. Good predictability was found on only 4 plots (all in the agricultural area, late season). Predicted 30-minute infiltration rates based on soil texture were all lower than 30-minute rates observed in the field. There are limitations when soil texture predictive methods developed for agricultural lands are used to describe infiltration patterns on both native and converted rangelands. Given the current state-of-the-art, if infiltration rates are important, they should be measured in the field using appropriate methodologies.

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Trace element intake via soil ingestion in pronghorns and in black-tailed jackrabbits

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Abstract

Soil ingestion ratios were estimated for 2 primary herbivore species utilizing a sagebrush ecosystem in southeastern Idaho to determine the relative importance of soil and vegetation pathways in trace element ingestion and to make predictions of the importance of these pathways for toxic and radioactive elemental intake. The mean ($\bar{x}$ and 95% CI) soil intake rates for pronghorns *(Antilocapra americana)* and black-tailed jackrabbits *(Lepus californicus)* were 48.7 (45.0–52.7) and 9.7 (9.0–10.6) g/day, respectively, with seasonal peaks occurring in spring (March–May) and in fall (August–October). We did not determine whether soil intake resulted from direct soil ingestion or soil attachment to ingested forage. Soil comprised 5.4% and 6.3%, respectively, of the pronghorn and jackrabbit total dry matter intake. Relating trace element concentrations in soil and vegetation to the daily soil and forage intake rates permitted an estimate of the importance of these 2 ingestion pathways. For both pronghorn and jackrabbits, the estimated percentage of elemental intake attributable to soil was 75% (Na, Fe, V, and F) and 10–50% (Mn, Cr, Mg, Ni, K and Zn).

Key Words: *Antilocapra americana*, black-tailed jackrabbit, environmental contaminants, *Lepus californicus*, nutrition, pronghorn, soil ingestion, trace elements

Weeks and Kirkpatrick (1976) and Salter and Pluth (1980) documented seasonal variation in soil or grit intake by white-tailed deer *(Odocoileus virginianus)*, fox squirrels *(Sciurus niger)*, woodchucks *(Marmota monax)*, and feral horses. These studies related soil or grit ingestion to increased demand for sodium, primarily during the spring. Few previous studies have dealt with the quantity of soil ingested by wildlife (Skipworth 1974, Arthur and Alldredge 1979), and only minimal information exists on the importance of soil in trace element intake.

We initiated research in December 1980 on the 8,310-km² Idaho National Engineering Laboratory (INEL) in southeastern Idaho to determine the mass of soil ingested seasonally by pronghorns and black-tailed jackrabbits. In conjunction with research on pronghorn and jackrabbit food habits at the study site, vegetation dietary components and soil samples were analyzed for trace elements. Comparisons of the quantities of trace elements ingested via soil and vegetation intake were made based on the concentrations of these elements in soils and vegetation. This paper presents an indirect method to determine the masses of soil ingested by pronghorn and black-tailed jackrabbits in southeastern Idaho and evaluates the potential importance of this intake mechanism for ingestion of trace elements.

Study Area

The study area, elevation 1,460–1,650 m, encompassed 300 km² of the west central portion of the INEL, 16 km south of Howe, Butte County, Idaho. Surface soils along the west boundary of the study area are slightly calcareous loams derived from loess and limestone alluvium deposited from the Lost River Range. The remainder of the study area (approximately 90%) is a thin loess-covered basalt plain. Surface soils in this area are silt loam and rocky silt loam and are noncalcareous to slightly calcareous. Vegetation associated with alluvial soils is dominated by big sagebrush *(Artemisia tridentata)*, winterfat *(Ceratoides lanata)*, and green rabbitbrush *(Chrysothamnus viscidiflous)*. Two vegetation types occurred on the remainder of the study area, a big sagebrush-green rabbitbrush-bottlebrush squirreltail *(Elymus elymoides)* type and a big sagebrush-bluebunch wheatgrass *(Pseudoroegnaria spicatum)*-green rabbitbrush type (McBride et al. 1978). Giant wildrye *(Leymus cinereus)* occurred in isolated stands throughout the study area.

The estimated density of jackrabbits on the northwest section of

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the study area was 2.9/ha throughout most of the study (R.J. Gates, unpubl. data), and the population was thought to be a cyclic peak in 1981 (Anderson and Johnson 1983, Stoddart 1983). Pronghorns used the study area primarily during the winter and spring but were observed there throughout the study period. During the winter and early spring of 1981, 200–300 pronghorns were observed on the southwest section of the study area.

Methods

We estimated the quantity of soil ingested by determining titanium concentrations in soil, vegetation, and feces. The experimental approach has been described previously by Healy (1968) and Mayland et al. (1975), and is based on the premise that titanium is relatively abundant in soil (1,000 to 3,000 ppm) and is not metabolized by vegetation or animal tissues (usually <1 ppm). Low concentrations of titanium in animal tissues and vegetation supported this contention. Because titanium found in fecal material results from soil intake (Mayland et al. 1975), concentrations of titanium in feces and soil provide an estimate of the animal's soil intake rates.

Twenty surface (0–5 cm) soil samples and 28 vegetation (big sagebrush leaves and grass composites) samples were collected in May 1982. Between December 1980 and November 1981, 10–19 pronghorn pellet groups and 7–14 jackrabbit fecal samples were collected monthly. Only recently deposited feces were collected and samples were collected opportunistically within the study area. Pronghorn samples were collected by observing animals in the study area and searching utilized areas for fresh fecal samples; whereas jackrabbit samples were collected throughout the entire area. Metacarpel bone, muscle, liver, and kidney samples were obtained from 10 jackrabbits collected from the study area in November 1980 and April 1981 and from 7 road-killed pronghorns.

All animal tissue, vegetation, and fecal samples were ultrasonically washed in demineralized water for >0.5 hour to remove surface-attached soil particles. Fecal samples also were scrubbed with a brush to facilitate removal of surface soil contamination. A minimum of 20% of the fecal pellets were viewed microscopically to assure removal of surface-attached soil particles. Samples were oven-dried for 72 hours at 70° C, screened through a 2-mm mesh screen and sent to a commercial laboratory where they were acid digested (combination of nitric and perchloric acid), and analyzed for titanium by flame atomic absorption (S. Moore, pers. commun.). The lower detection limit for Ti in soil and animal tissues and in vegetation was 10 ppm and 0.6 ppm, respectively. Twenty percent of the samples were analyzed in duplicate to assure consistency in spectrophotometer readings. National Bureau of Standards reference samples were analyzed for quality assurance.

Estimates of the quantity of soil ingested were derived from the following model:

$$S_{day} = \frac{({}^{F}Ti \times {}^{F}day) - ({}^{V}Ti \times {}^{V}day)}{S_{Ti}}$$

where

${}^{S}day$ = soil mass (g) ingested/day,
${}^{F}Ti$ = titanium concentration (μg/g) in feces,
${}^{F}day$ = dry weight (g) feces defecated/day,
${}^{V}Ti$ = titanium concentration (μg/g) in vegetation,
${}^{V}day$ = dry weight (g) vegetation consumed/day, and
${}^{S}Ti$ = mean titanium concentration (μg/g) in surface soil.

We used an average daily forage intake (dry wt) of 145 g for black-tailed jackrabbits (Arnold and Reynolds 1943) and 850 g for pronghorns (Severson et al. 1968) to estimate soil ingestion. We assumed dry matter digestibilities of 43% for diets of jackrabbits (Arnold and Reynolds 1943) and 54% for pronghorns (Welch et al. 1983). Based on these assumptions, the mean daily defecation rates used in the model were 82 for jackrabbits, 391 g/day for pronghorns.

Mean soil ingestion rates were calculated for each month. One-way analysis of variance was used to determine significant differences in soil intake rates among months. A significance level of $P<0.05$ was used for rejection of the null hypothesis. Duncan's new multiple range test (Duncan 1955) was used to separate statistically different means.

Soil and vegetation samples were analyzed for Ca, Cr, Cu, F, Fe, K, Mg, Mn, Na, Ni, P, V, and Zn by a conductively coupled argon plasma spectrograph. Minimum detection limits (ppm) for these elements in soil were Ca (10), Cr (0.5), Cu (1), F (10), Fe (20), K (1), Mg (20), Mn (10), Na (10), Ni (1), P (10), V (1), and Zn (5). Mean concentrations of the 13 elements in soil and vegetation were multiplied by mean daily soil and vegetation intake rates. The percentage of daily intake of each element was compared for soil vs. vegetation consumption for both pronghorns and black-tailed jackrabbits.

Results

Titanium concentrations in surface (0–5 cm) soils at the study area ranged from 3,770 to 6,140 ppm with a mean ($\bar{x}$ ± SD) of 5,280 ± 715 ppm (Table 1). Because pronghorns were observed over the entire study area, this mean was used to calculate the pronghorn soil intake rate. However, because we collected all black-tailed jackrabbit feces near the northwest portion of the study area, we used the mean titanium concentration of soils in this area (4,315 ± 432 ppm) to determine jackrabbit soil intake rates.

Table 1. Titanium concentration (ppm) in soil, vegetation and animal tissue on the Idaho National Engineering Laboratory in southeastern Idaho.

Media	$\bar{x}$ + SD	n	Range
Soil	5280 ± 715	20	3770 - 6140
Sagebrush leaves	24.9 ± 4.9	18	18 - 33
Grass Composites	18.7 ± 7.8	10	10 - 29
Pronghorn			
Muscle	BDL*	6	-
Liver	BDL	7	-
Bone	BDL	7	-
Kidney	BDL	7	-
Feces	851.3 ± 363.8	177	150 - 2200
Jackrabbit			
Muscle	13.5 ± 20.2[+]	6	BDL - 43
Liver	29.5 ± 31.6	5	BDL - 82
Bone	21.6 ± 17.5	6	BDL - 52
Kidney	15.1 ± 17.6	6	BDL - 37
Feces	607.7 ± 250.4	118	200 - 1630

*BDL = Below detection limits (≤0.6 ppm)

[+] 0.6 ppm used to calculate the mean when the sample value was below detection limit.

Titanium concentrations in washed vegetation samples collected at the study area ranged from 10 to 29 ppm for grass ($\bar{x}$ ± SD = 18.7 ± 7.8) and 18–33 ppm for sagebrush leaves ($\bar{x}$ ± SD = 24.9 ± 4.9). The overall mean concentration of 20 ppm titanium was used for forage (V_{Ti}) in the soil ingestion rate model.

Titanium concentrations in all pronghorn muscle, liver, bone, and kidney tissue samples were below the lower detection limit of 0.6 ppm, indicating little or no tissue absorption of this element. Some jackrabbit tissues had higher titanium concentrations than the pronghorn tissues (Table 1). The reason for these elevated concentrations was unknown.

Because microscopic examination of washed pronghorn and jackrabbit fecal pellets revealed no surface attachment of soil particles, the reported titanium concentrations for feces were assumed to be from soil in feces and not surface contamination. Titanium concentrations in washed jackrabbit and pronghorn fecal samples ranged from 200 to 1630 and 150 to 2200 ppm, respectively (Table 1).

The annual mean ($\bar{x}$; 95% confidence interval) daily soil intake rate estimated for pronghorn was 48.7(45.0–52.7) g/day.

Table 2. Mean elemental concentrations (ppm) in surface soil and washed vegetation samples on the Idaho National Engineering Laboratory in southestern Idaho.

Media		Concentration (ppm)					
		Ca	Cr	Cu	Fe	Mg	Mn
Soil	x ± SD	16944 ± 10892	43.4 ± 7.3	21.5 ± 4.1	21033 ± 2694	7631 ± 1173	402 ± 79
(n = 12)	Range	6370 - 37700	33.8 - 54.5	16.2 - 28.5	17400 - 26300	5450 - 9450	295 - 520
Grass	x ± SD	15362 ± 5383	7.9 ± 1.9	16.7 ± 14.3	530 ± 313	2244 ± 469	56.4 ± 14.8
(n = 6)	Range	7010 - 21500	6.8 - 10.7	8.9 - 42.2	333 - 1070	1850 - 3010	40.7 - 78.0
Sagebrush Leaves							
(n = 11)	x ± SD	8554 ± 1983	4.0 ± 2.5	17.1 ± 2.1	216 ± 60	1709 ± 323	35.9 ± 6.9
	Range	6300 - 12200	BDL* - 8.0	13.5 - 20.9	122 - 285	1030 - 2120	27.6 - 47.6

Media		Concentration (ppm)						
		Ni	P	V	Zn	F	Na⁺	K⁺
Soil	x ± SD	23.2 ± 2.7	3597 ± 738	45.9 ± 6.2	81.4 ± 12.3	519 ± 132	10643 ± 1400	22528 ± 1100
(n = 12)	Range	20.6 - 29.1	2780 - 5530	39.3 - 61.1	68.1 - 102	300 - 800	8300 - 12300	21000 - 23700
Grass	x ± SD	10.0 ± 3.7	10876 ± 2889	0.2 ± 0.5	41.4 ± 18.3	30.3 ± 9.6	54 ± 52	7960 ± 1170
(n = 6)	Range	6.5 - 12.6	8160 - 14000	BDL - 1.2	22.9 - 69.4	14.0 - 45.0	BLD - 176	5900 - 10700
Sagebrush leaves								
(n =11)	x ± SD	6.7 ± 6.2	7777 ± 2011	BDL	29.2 ± 8.8	16.9 ± 11.6	74 ± 84	15900 ± 1100
	Range	2.5 - 21.6	3270 - 10100	——	18.7 - 51.4	2.0 - 38.9	BLD - 461	13500 - 17700

*BLD = Below minimum detection limits for this element.

⁺n = 7, 24 and 32 for soil, grass, and sagebrush, respectively for the elements Na and K.

Pronghorn soil intake rates differed significantly ($P<0.001$) between months, ranging from 21.5 g/day in June to 84.0 g/day in March (Fig. 1). Monthly soil intake rates were highest ($P<0.05$) during March–May, and August–October.

The annual mean ($\bar{x}$; 95% confidence interval) daily soil intake rate estimated for black-tailed jackrabbits was 9.7(9.0–10.6) g/day. Jackrabbit soil intake rates also varied significantly ($P<0.001$) between months. The highest soil intake rate was observed in December, with significant ($P\leq0.05$) peaks also occurring in March–May and in September and October (Fig. 1).

Elemental Intake Due to Soil Ingestion

Mean concentrations of Ca, Cr, Cu, F, Fe, K, Mg, Mn, Na, Ni, P, V, and Zn in soils and vegetation at the study area are presented in Table 2. Multiplying the forage and mean annual soil intake

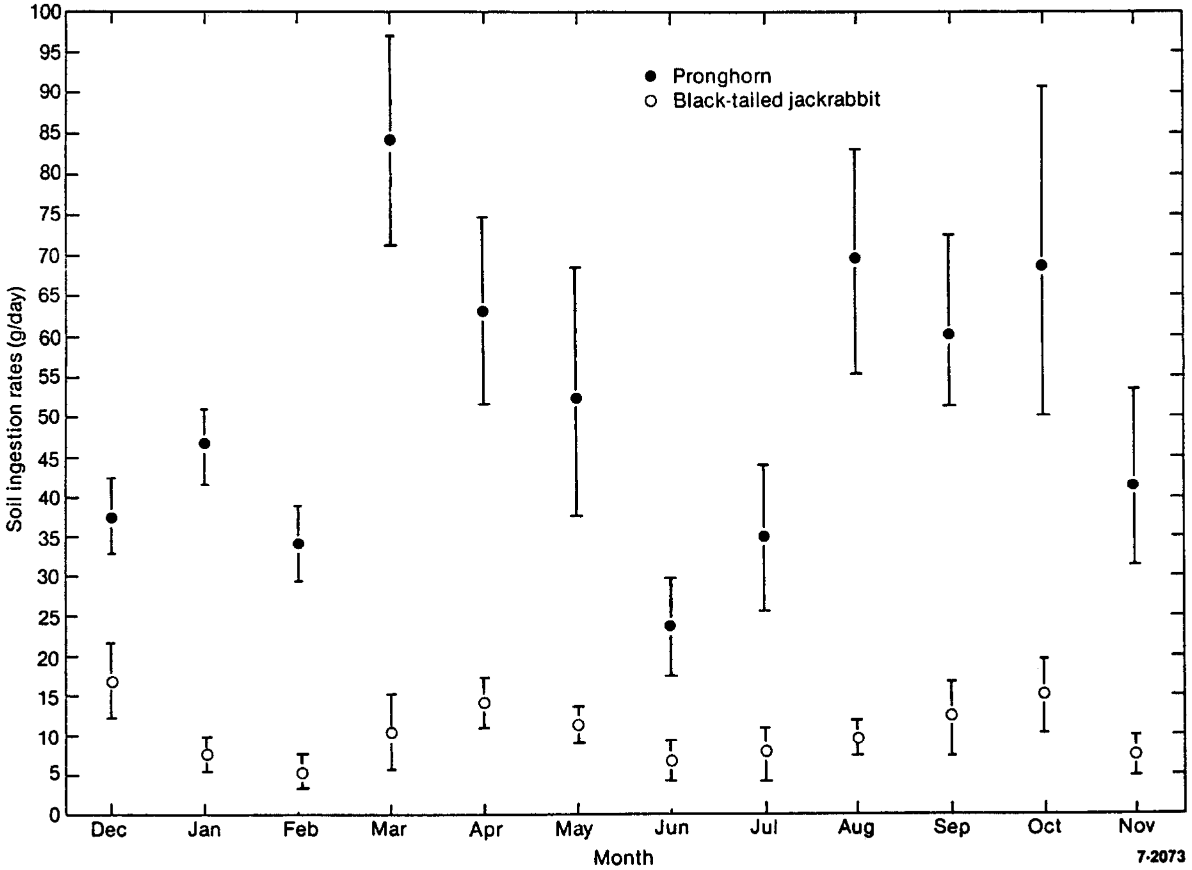

Fig. 1. *Daily soil ingestion rates ($\bar{x}$, 95% CI) for black-tailed jackrabbits and pronghorns in southeastern Idaho during December 1980 through November 1981.*

rates of 85 and 48.7 g/day (pronghorn) and 145 and 9.7 g/day (jackrabbit) by the mean concentration of elements in each medium provided an estimate of the percentage of the daily intake of elements resulting from soil versus forage intake (Fig. 2). Due to high occurrence of shrubs in pronghorn and jackrabbit diets on the study area (Gates, unpublished data), concentrations of elements in sagebrush leaves (Table 2) were used for the forage category.

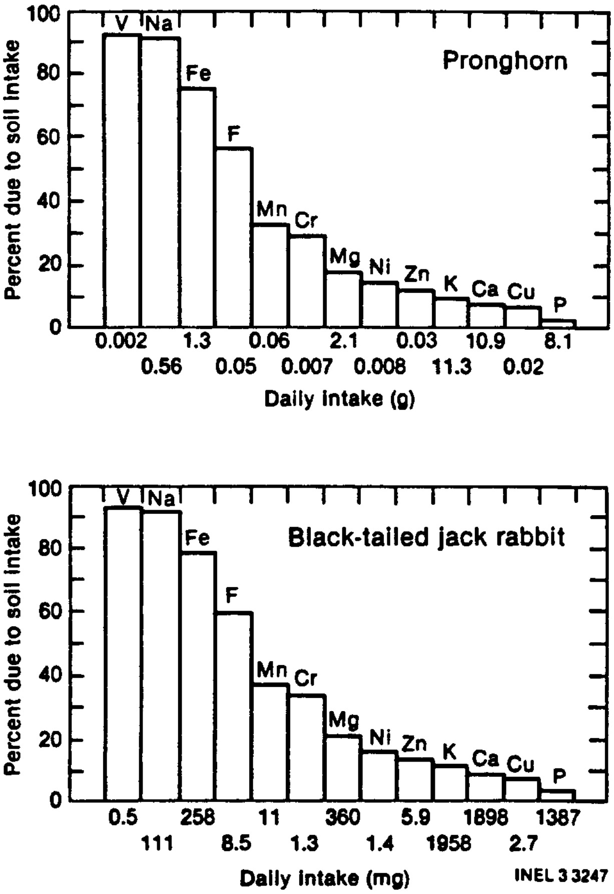

Fig. 2. *Percentage of daily elemental intake of elements due to soil ingestion and estimated daily mass of each element ingested by pronghorns and black-tailed jackrabbits on the Idaho National Engineering Laboratory.*

Because soil comprised similar percentages of the total dry matter ingested by pronghorns (5.4%) and jackrabbits (6.3%), the overall percentage of the daily intake of elements resulting from soil ingestion was similar for these 2 species (Fig. 2). Soil ingestion resulted in a majority (>50%) of the daily intake of the elements Fe, V, Na, and F for pronghorns and jackrabbits. Greater than 30% of the intake of Cr, and Mn was from soil ingestion. Vegetation ingestion resulted in greater than 90% of the daily intake of the elements Ca, Cu, and P.

The total quantities of elements ingested via soil and forage intake were estimated by multiplying the mass of these media ingested by the respective mean concentrations of each element (Fig. 2). For pronghorn, the estimated daily Na, K, Ca, P, and Mg intake via soil and vegetation ingestion was 0.56, 11.3, 10.9, 8.1, and 2.1 g. Daily consumption of the trace elements Cr, V, and Ni was 0.007, 0.002, and 0.008 g. Jackrabbit daily intake of the trace elements ranged from 0.0005 g V to 1.9 g K (Fig. 2).

Discussion

The methods we used to determine seasonal soil intake rates by pronghornsand black-tailed jackrabbits were based on the premise that high concentrations of titanium occur in soils, and titanium is not assimilated by vegetation or animal tissues. At our study area, titanium concentrations in soil exceeded previous reports, ranging from 3,760 to 5,260 ppm. Also, the titanium concentrations detected in sagebrush leaves and grass samples were higher than the reported level of 1 ppm for vegetation (Healy 1968, Healy et al. 1970, Mayland et al. 1977). Higher titanium concentrations in vegetation may have been attributable to very fine soil particles remaining on vegetation after washing (Skinner 1982). A mean of 20 ppm titanium in vegetation was used in the soil ingestion rate calculations to correct for titanium in forage; however, if we had used 1 ppm titanium in vegetation, the mean soil intake rates would have increased only from 5 to 13% for pronghorns and from 4 to 10% for black-tailed jackrabbits.

Mean ($\bar{x}$; 95% confidence interval) daily soil intake rates for pronghorns and black-tailed jackrabbits were 48.7 (45–52.7) and 9.7 (9.0–10.6) g soil/day. Soil comprised 5.4 and 6.3% of the total daily dry matter intake for pronghorns and jackrabbits. These percentages are greater than the 0.6 to 2.1% of the dry matter intake estimated for mule deer in northcentral Colorado (Arthur and Alldredge 1979) and greater than 2% of the dry matter intake estimated for cattle in New Zealand (Healy et al. 1970). Mayland et al. (1977) estimated that soil comprised 7% of dry matter intake for cattle feeding on Idaho grassland.

Monthly soil intake rates calculated in this study indicated 2 seasonal peaks in soil ingestion by pronghorns and jackrabbits. Mean soil intake rates during March through May increased 73% over the previous 2 months for jackrabbits and 93% over the previous 3 months for pronghorns. Soil intake by jackrabbits was relatively low during June through August, but increased 76% to a second peak in September and October. An anomalous peak occurred in December 1980 when jackrabbit soil intake was 110 and 140% higher than in January and November 1981, respectively. Similar to those for jackrabbits, a second peak occurred during August and October when mean intake increased 130% over June and July. Pronghorn soil intake returned to a relatively low level in November.

We cannot explain monthly trends in soil intake rates because direct observations of pronghorns and jackrabbits consuming soil were rare. One possible reason for lower soil intake rates during winter months was the existence of snow cover. Average monthly snow depth was low during the period when fecal samples were collected with 17.5, 21.6, 2.5, and 2.5 cm snow in December 1980 and January, February, and March 1981. The months of peak snow depth were the same as the months when lower soil intake rates occurred for pronghorns. For jackrabbits, however, this was not true, since in December when the snow depth was 17.5 cm the highest soil intake rate of 8.4 ± 3.5 g/day was obtained. For jackrabbits, it appears that decreases in soil intake rates were not associated with snow depths.

Tame mule deer *(Odocoileus hemionus)* feeding in northcentral Colorado had higher soil intake rates in spring than during other seasons, because they consumed soil attached to roots of new growth grasses and forbs (Arthur and Alldredge 1979). Similarly, we observed new growth of forbs in late April and May (J.E. Anderson, pers. commun.), during which time soil intake rates for jackrabbits and pronghorns were high. Examination of pronghorn fecal samples (R.J. Gates, unpubl. data) indicated that forbs comprised 41% of the May diet, whereas in the preceding 6 months forbs never comprised greater than 6% of the fecal fragments. Therefore, soil intake rates in March and April (months when sagebrush comprised greater than 90% of the diet) resulted from direct consumption of soil or attachment of soil to sagebrush leaves.

Soil ingestion by jackrabbits may have been related to the proportion of phlox *(Phlox hoodii)* and winterfat in the diet (R.J. Gates, unpubl. data). Ninety-nine jackrabbit fecal samples were analyzed for titanium concentrations and the occurrence of plant tissue fragments. Titanium concentration was correlated with percent of phlox and winterfat fragments in fecal samples (r=0.91, ≤0.01). During vegetation collections, we noted a large amount of soil attachment on the surface of phlox and winterfat. The low growth forms of winterfat and of phlox may have caused indirect soil intake when they were eaten.

Skipworth (1974) suggested that animals may consume soils as a source of trace elements when vegetation lacks these elements. The peaks in pronghorn and jackrabbit soil intake which we observed during March through May coincided with maximum salt lick use by white-tailed deer in southern Indiana that was necessitated by increased sodium requirements during the spring (Weeks and Kirkpatrick 1976). Obligatory intake of large amounts of potassium and water with succulent forage during spring may result in a negative sodium balance, which could be corrected by forage consumption, because plants contained low sodium concentrations (Weeks and Kirkpatrick 1976). Our soil samples contained high levels of Na and K compared to grass and sagebrush leaves (Table 2). The Na:K ratio of soil was 0.47 while the same ratios were 0.0056 in grass and 0.0039 in sagebrush leaves. We observed spring and fall peaks in soil intake by pronghorns and jackrabbits, similar to peaks in Na-drive observed in fox squirrels and woodchucks by Weeks and Kirkpatrick (1978). Our results resemble the findings of Weeks and Kirkpatrick (1976, 1978) in that soil ingestion by pronghorns and jackrabbits could have offset a high dietary intake of K, especially during spring and fall when vegetation resumes growth after dormancy. Excessive dietary K may interfere with otherwise efficient Na-conserving mechanisms of herbivores. Approximately 92 and 93% of daily Na intake by pronghorns and jackrabbits was attributable to soil ingestion.

Regression analysis used in our study provided an estimate of the importance of soil ingestion in elemental intake by pronghorns and jackrabbits. For the elements Fe, V, Na, and F, greater than 50% of the estimated daily intake was attributed to soil ingestion. Data collected over the last 25 years indicates that in addition to Fe, F, and V are also essential nutrients for animals (Miller and Neathery 1977). Similarly, soil intake resulted in 10–50% of the daily intake of the elements Cr, Mg, Mn, Ni, and Zn. The availability of the soil ingested elements for animal tissue assimilation is unknown. However, ingested soil is subject to a wide variety of digestive processes such as pH changes, bacterial breakdown, and complexing agents. Some microelements are absorbed into animal tissue directly from ingested soil (Healy et al. 1970). In addition to soil ingestion functioning as a major intake mechanism for trace elements, it is also likely an important pathway for intake of environmental contaminants such as radionuclides, herbicides, and insecticides (Healy 1973).

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Simple pivot balance for measuring phytomass in quadrats

D.E. JOHNSON, M.M. BORMAN, AND MOHAMED BEN ALI

Abstract

An inexpensive, easily constructed balance was made to measure plant phytomass from clipped quadrats. It can be fabricated from materials generally available in developing countries and, within the designed range, it is accurate enough to provide reliable estimates of standing crop. Since balances are easily and inexpensively constructed they can be made in quantity and distributed to local extension agents and farmers.

Key Words: vegetation sampling, biomass estimation

In the developing world there is a need for rational utilization of rangeland resources. This requires that managers have a clear understanding of availability and yield of plants eaten by livestock throughout the seasons. We commonly use quadrats and gram or pencil shaped scales to estimate the standing crop. The values obtained are then averaged to calculate an estimate of the grazing days allowable. Quadrats are easily constructed in developing countries but relatively expensive pencil scales ($30–$45) must be imported. To overcome this limitation and to make the materials necessary for accurate estimation of phytomass more readily available to extension agents, we constructed a simple pivot balance.

This balance consists of a flat piece of metal, preferably aluminum or something else that is inoxidizable. The piece is cut as shown in Figure 1 and holes are drilled for a fulcrum wire, a clip wire, and an indicator wire. Holes should be large enough to permit the wires to move freely, yet small enough to maintain the wire in a fixed position. Hard metal wires are then inserted into the holes and bent over the back of the plate so that they cannot fall out but move freely.

The balance is then calibrated against standard weights. We use standard weights calibrated on a triple beam balance in our laboratory to indicate the position of the indicator wire for 5-g intervals. Marks are then either etched into the metal of the balance or drawn on a piece of paper that has been pasted to the face of the balance (Fig. 1). Finer division marks can be drawn within these 5-g intervals using a scaled ruler.

As can be seen in Figure 1, the distance between the marks is not uniform (because the scale pivots). As a result the relative accuracy of the balance is not uniform across its range; however, it is possible to construct an accurate balance within the desired range by changing the position of the pivot hole or by using a heavier or lighter metal plate. With proper construction, a balance that provides good readings for the desired range can be obtained.

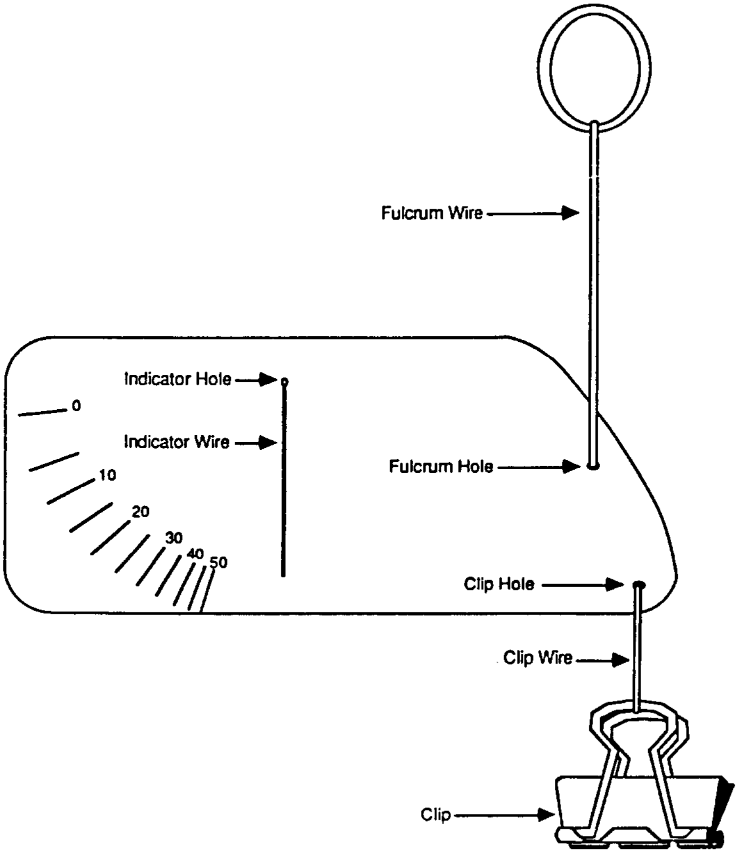

Fig. 1. *A simple pivot balance for measuring vegetation in quadrats.*

At the time of this work authors were assistant professor and instructor, Department of Rangeland Resources, Oregon State University, Corvallis 97331; and director, Central Tunisia Rangeland Development Project Office de L'Elevage es des Paturages, Kairouan, Tunisia, respectively.

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In order to test the potential accuracy of this type of balance and to compare it with a standard 100-g pencil scale, we constructed a 50-g balance and calibrated it to the nearest gram. Sixty samples ranging between 2 and 49 g were weighed on the pivot balance, the pencil scale, and a laboratory balance accurate to the nearest 0.01 g. Weights, as measured by the laboratory balance, were highly correlated to both the pivot balance and the pencil scale (correlation coefficients of 0.9998 and 0.9999 respectively). More important than the correlation is the error across the measured range. The average absolute error was 0.195 g for the pivot balance and 0.139 g for the pencil scale. Maximum error for the 60 readings was 0.58 g for the pivot balance and 0.54 g for the pencil scale. Although the pivot balance as we construct it is not as accurate as the pencil scale, our test balance gave consistent readings with less than 1 gram error in the design range.

We work with rangelands that normally have standing crops of from 500 to 2,000 kg of green material/ha and sample with 0.25-m^2 quadrats. Therefore, we construct balances that weigh from 0 to 50 g and are small enough to fit in a shirt pocket. Our balances cost about $0.50 for materials and require about 40 minutes to construct and calibrate. This type of balance should be useful for range managers in many developing countries.

Collecting, drying, and preserving feces for chemical and microhistological analysis

RAY T. HINNANT AND M.M. KOTHMANN

Abstract

Chemical and botanical analyses of feces provide information on diet quality and composition that is not easily collected directly from a grazing animal. However, fecal excreta is readily available in the pastures the animals are grazing. This study was conducted to determine the feasibility of collecting fecal samples from the pasture for chemical (nitrogen) and botanical analysis. Two experiments were conducted to determine the effects of method of drying (oven-dried vs. freeze-dried) and duration of fecal pat exposure on chemical and microhistological analyses. Concentration of nitrogen was not affected by method of drying or by duration of exposure in the field. Samples <72 hours during the winter and <24 hours during the summer may be used for nitrogen analysis. However, we recommend that samples be collected as soon as possible following defecation to reduce possible negative effects of precipitation, insect damage, and trampling. Method of drying had no significant ($P<0.05$) effect on percentage of identifiable fragments or subsequent forage class determination. Bleach, as a blending medium reduced pigment masking of epidermal fragments resulting in an increase in the percentage of identifiable epidermal fragments. Duration of exposure did not affect identification of most of the forage classes. The proportion of identifiable fragments, was lower during winter than summer.

Key Words: nitrogen, fecal nitrogen, diet quality, microhistological analysis, fecal analysis

The nitrogen content of feces has frequently been used to predict diet quality and nutrient intake of grazing ruminants. Fecal samples can also be analyzed to estimate botanical composition of the diet. Analysis of feces may yield much ecological information (Putman 1984). Use of fecal nitrogen to estimate nitrogen concentration of forage grazed by sheep may be more accurate than estimates obtained by analysis of cut herbage (Raymond 1948). Wofford et al. (1985) and Sinclair et al. (1982) also found a strong relationship between percentage of diet nitrogen and fecal nitrogen. Significant relationships exist between fecal nitrogen and the digestibility and intake of forage (Hutchinson 1958, Fels et al. 1959, Arnold and Dudzinski 1963, Renecker and Hudson 1985). The primary advantage of the fecal nitrogen technique is that there is no need to disturb, fistulate, or sacrifice the animals (Erasmus et al. 1978). The technique has further advantages if fecal samples could be collected from the pasture post defecation rather than as rectal samples.

Oven drying requires less time than freeze-drying, which may take 3–7 days. Freeze-drying substantially increases the cost of sample preparation for analyses and delays results. Harris (1970) defined oven-drying as 105° C until a constant weight and partial oven-drying as 60° C in a forced convection oven with about 12% moisture remaining. Freeze-drying is usually considered partial drying. Raymond and Harris (1954) found oven-drying unacceptable for accurate determination of fecal nitrogen and recommended analysis of fresh feces. Losses of nitrogen from −3 to 34% have been reported at oven temperatures of 65–100° C with varying drying times (Colovos et al. 1957, Bredon et al. 1961, Falvey and Woolley 1974). Partial-drying of feces at 60–65° C in a forced-draft oven resulted in nitrogen losses of 4–6% (Gallup and Hobbs 1944) or no loss (Forbes et al. 1946).

Two methods commonly used to estimate diet composition are microscopic examination of esophageal fistula and fecal samples. The latter technique was described by Baumgartner and Martin (1939), Sparks and Malechek (1968), and more recently modified by Holechek and Valdez (1985). This technique uses unique identifiable characteristics of epidermal cells as the basis of plant species identification. Identifiable features include size and shape of epidermal hairs, cell shapes, and crystals in epidermal cells (Sparks and Malechek 1968).

The proportion of epidermal fragments that can be identified is affected by the method of sample preparation and season of collection (Holechek 1982). Use of bleach (Williams 1969) and sodium hydroxide solutions (Vavra and Holechek 1980) can improve identifiable characteristics fecal samples by removing pigment masking from the cells. However, Holechek (1982) found bleach and sodium hydroxide may damage some plant material.

The first objective of this study was to determine the changes in nitrogen concentration of feces with duration of exposure. Feces were dried by 2 methods, partial oven-drying and freeze-drying.

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The second objective was to determine the effects of the 2 drying methods, the addition of bleach to the blending medium, and the duration of exposure on microhistological identification of plant fragments.

Methods

Experiments were conducted to evaluate effects of method of drying on chemical and physical constituents of fecal samples collected from the Sonora Research Station, Sonora, Texas, during winter and from the Native Plant & Animal Conservancy, College Station, Texas, during summer.

Method of Drying

The first experiment compared effects of freeze-drying and oven-drying on chemical and physical contents of fecal samples. These samples were collected from a herd of cows grazing in a short-duration grazing study. Two equal (300-g, fresh weight) sub-samples were taken from 5 fresh fecal pats for 5 days during January 1980. All samples were frozen with 2 hours following collection for preservation. One sub-sample was freeze-dried, and the other partially oven-dried at 60° C for 24 hours. Samples were ground through a Wiley mill fitted with a 1-mm screen prior to analysis.

A second experiment was conducted to detect chemical and physical changes over time in fecal pats on the ground. Fresh sample fecal pats were identified and the cows were moved to a different pasture to prevent trampling damage. Ten pats were staked and initial samples collected immediately after defecation. Identified pats were subsequently sampled at 6, 24, 48, and 72 hours after defecation at Sonora and at 6 and 24 hours at College Station. There were no fecal collections for the 48- and 72-hour periods during the summer because the pat was decimated by insect activity. The crust of the pat was avoided when possible. No measurable precipitation occurred during either collection period. Samples were stored, dried, and ground as in the previous experiment.

Chemical Analysis

Dry matter (105° C for 24 hours) and organic matter (550° C for 3 hours) were determined from sub-samples for each sample. Nitrogen was analyzed by the micro-Kjeldahl method (AOAC 1975). Nitrogen is reported on an oven-dry, ash-free basis.

Microhistological Analysis

Samples collected from experiments 1 and 2 were used to examine the effects of drying method, blending medium, and duration of exposure on microhistological fragment identification. Ground fecal samples from the method of drying and blending medium experiments were composited across 5 pats within drying method and days. Samples were composited across 10 staked pats within collection periods from the duration of exposure study. Half of the samples from each experiment were blended for 1 min with 95% ethanol and the slides prepared with Hertwigs and Hoyers solutions (Sparks and Malechek 1968). The other set of samples was blended for 1 min with sodium hypochlorite (household bleach) and then slides were prepared as above. Five slides were made from each sample and 10 fields per slide were read by personnel at the diet laboratory at Texas Tech University (Scott and Dahl 1980). Total fragments in each field were counted. Fragments were placed into 3 categories: identifiable epidermal fragments, non-identifiable epidermal fragments, and non-epidermal fragments (NE). These categories were chosen to determine the effects of method of drying, blending medium, and duration of exposure on the proportion of identifiable and non-identifiable fragments. Identifiable fragments in each field were counted and recorded according to plant category. Plant categories were: warm-season perennial grasses, cool-season perennial grasses, forbs, browse, and cacti. Non-identifiable epidermal fragments were further categorized as: *Lacked characteristics*-The fragment was large enough and was not damaged, but there were not enough identifiable characteristics present to make a positive identifications; *Pigment*-Tissue was identified as epidermal but pigment masked the identifiable characteristics; *Damaged*-Epidermal fragments were too small or mutilated to be identified.

The proportion of NE fragments was calculated as NE fragments divided by total number of fragments. The proportion of identifiable fragments was calculated as identifiable fragments divided by total epidermal fragments. Proportion data were transformed prior to statistical analysis by an arc-sine, square root transformation developed for binomial proportion data (Snedecor and Cochran 1980). Data were analyzed statistically by general linear model (GLM) procedures (SAS 1982). Mean separation was performed using Duncan's (1955) multiple range test.

Results and Discussion

Chemical Analysis

Method of Drying

We observed no significant differences ($P<.05$) in nitrogen content of oven-dried (1.35% N) or freeze-dried (1.38% N) feces. Oven-drying fecal samples reduced sample preparation time for chemical analysis. Lower temperatures (<60° C) and an oven with a high air flow is recommended to prevent the detrimental effect of high temperatures combined with high moisture for long durations in the oven (Raymond and Harris 1954).

Duration of Exposure

Mean nitrogen content of feces collected fresh through 72 hours in winter (1.2% N) and fresh through 24 hours in summer (1.8% N) was not affected ($P<0.05$) by duration of exposure. It is difficult to determine the age of a fecal pat in a pasture. Fecal pats tend to be extremely moist when forage is actively growing and dry when forage is dormant because of varying moisture content of forages. Observations of fecal pats in the pasture over a few days should allow a person to estimate the approximate age of the pat.

Because there was no effect of exposure time on fecal nitrogen content during winter or summer, age of pat should be of little consequence for fecal nitrogen monitoring within the sampling periods reported in our study. However, it is recommended that samples analyzed for chemical analysis be collected at defecation or as soon thereafter as possible to avoid possible effects of precipitation, trampling, insect loss or addition, and crusting.

Microhistological Analysis

Method of drying

Drying method had no effect on the percentage of NE fragments ($P<0.05$) (Table 1). Approximately 46% of the fragments in all samples were not epidermal, or were unrecognizable as epidermal fragments. Method of drying had no effect on percentage of identifiable or non-identifiable epidermal fragments, or any of the diet categories when averaged across blending mediums. Samples which were oven-dried had approximately twice the non-identifiable epidermal fragments in the pigment category as compared to freeze-drying. Oven-drying of frozen samples appeared to "bleed" the pigment during defrosting onto other unidentifiable characteristic, especially those fragments which lacked adequate characteristics and damaged epidermal fragments (Table 1). Non-identifiable cells placed into the damaged category in the freeze-dried samples were increased ($P<0.05$) due to a reduction in pigment masking rather than the drying method. Freezing of samples, weathering of dormant vegetation, and mastication prior to consumption were suspected of causing the high proportion of damaged epidermal cells with both drying methods.

Blending Medium

Use of bleach in sample preparation increased the percentage of identifiable and NE fragments and decreased the percentage of non-identifiable fragments ($P<0.05$) (Table 1). Bleach treatment allowed an approximate 15% increase in the recognition of some identifiable epidermal and NE fragments masked by pigmentation

Table 1. Mean percentages of non-epidermal and identifiable and non-identifiable epidermal fragments in two drying methods and two blending mediums.

Category	Drying method		Blending medium	
	Oven-dried	Freeze-dried	Bleach	Ethanol
NE	45.5	46.3	51.8^x	40.0^y
Identifiable	12.2	12.1	14.1^x	10.2^y
Non-identifiable	42.3	41.6	34.1^x	49.8^y
	Identifiable epidermal fragments			
Warm season grass	62.9	58.3	60.7	60.5
Cool season grass	18.7	20.2	20.1	18.8
Browse	9.7	11.4	8.3	12.8
Forbs	1.8	2.8	2.7	1.9
Cactus	6.9	7.3	8.2	6.0
	Non-identifiable epidermal fragments			
Too much pigment	30.4^a	17.4^b	11.1^x	36.7^y
Lacked adequate characteristics	4.2^a	11.0^b	6.5	8.6
Damaged	65.4^a	71.6^b	82.4^x	54.6^y

^{a,b,x,y}Means in the same row within drying method and blending medium experiments, not followed by the same letter are significantly different ($P<.05$).

which otherwise would have been included in one of the non-identifiable epidermal fragment categories. These results appear to support the findings of Williams (1969) and Vavra and Holechek (1980). They found bleach and sodium hydroxide reduced the number of unidentifiables due to pigment and allowed more fragments to be identified. Holechek (1982) also found an increase in identifiable fragments of samples treated with bleach.

There was no difference in the calculated percentage of diet categories using either blending medium (Table 1). The percentage of non-identifiable fragments due to too much pigment was reduced ($P<.05$). Bleach reduced fragment masking resulting in an increase in identifiable fragments and an increase in the damaged category ($P<.05$). Holechek (1982) reported bleach damaged epidermal cells. The increased proportion of damaged epidermal cells when bleach was used resulted from a shift of fragments from the category of too much pigment into the damaged category.

Duration of Exposure

Duration of exposure significantly ($p<.05$) affected the percentages of NE and non-identifiable epidermal fragments at both locations (Sonora and College Station) and identifiable epidermal fragments at College Station (Table 2). However, there was no discernable trend for any of the plant categories with increased exposure. Significant difference for browse at Sonora and forbs at College Station probably resulted from sampling variation within the fecal pat. Percentages of warm-season grass, cool-season grass, and browse were not affected by the duration of exposure through 24 hours at College Station and warm-season grass, cool-season grass, forbs, and cacti through 72 hours at Sonora.

The season in which samples were collected appeared to have the greatest effect on percentage NE, identifiable, and non-identifiable characteristics (Table 3). Samples collected in winter at Sonora had a higher percentage of NE fragments in the feces. Weathering of winter forage was believed to have caused a reduction in the proportion of epidermal cells. The proportion of identifiable fragments was approximately 10 times greater during the summer collection period compared to the dormant, weathered forage eaten during winter. Fragments which lacked adequate characteristics were higher ($p<0.05$) for summer samples from College Station; however, the percentage of non-identifiable epidermal cells which were categorized as damaged was significantly greater from winter samples ($p<0.05$) than samples collected in the summer. It is possible that samples were damaged by freezing prior to analysis, but the large difference due to season points to weathering as the major cause. Weathering breaks down cell structure and identifiable characteristics. Holechek (1982) also reported higher ratios of identifiable fragments in samples collected in summer compared to other seasons except with horse diets. He reported 80–90% unidentifiable fragments from winter diets of deer and fall prepared diets compared to 40% unidentifiable fragments from summer diets of cows. The technician reading the samples could not ascertain the excact causes of the damage to the cells.

Table 2. Percentages of forage classes and percentages of non-epidermal and identifiable and non-identifiable epidermal fragments for varying durations of exposure (hours) at two locations.

Sonora	Duration of exposure				
	0	6	24	48	72
Warm season grass	70.2	75.7	81.7	69.8	55.3
Cool season grass	9.9	6.6	10.4	15.8	7.8
Browse	9.3^{ab}	14.4^{ab}	5.4^a	3.7^b	20.9^b
Forbs	2.9	2.0	2.5	5.7	14.6
Cactus	7.7	1.4	0	5.0	1.3
NE	39.7^b	51.0^a	38.0^{bc}	33.4^c	41.2^b
Identifiable	2.3	2.9	1.9	1.4	2.4
Non-identifiable	58.0^b	46.2^c	60.0^b	65.2^a	56.4^b

College Station	Duration of exposure		
	0	6	24
Warm season grass	2.0	3.2	8.3
Cool season grass	0	0	0
Browse	73.0	65.3	70.7
Forbs	24.9^{xy}	31.6^x	21.0^y
NE	33.5^y	34.2^y	41.1^x
Identifiable	22.6^x	24.8^x	14.6^y
Non-identifiable	43.9	41.0	44.3

^{a,b,x,y}Means in the same row not followed by the same letter are significantly different ($P<.05$).

Table 3. Effects of season of collection on the mean percentages of identifiable and non-identifiable epidermal fragments and non-epidermal (NE) fragments.

	Season	
	Summer	Winter
NE	36.3^a	40.7^b
Identifiable	20.6^a	2.1^b
Non-identifiable	43.1^a	57.2^b
	Non-identifiable epidermal fragments	
Too much pigment	24.7	19.4
Lack adequate characteristics	18.6^a	1.4^b
Damaged	56.7^a	79.2^b

^{a,b}Means in the same row not followed by the same letter are different ($P<.05$).

Conclusions

Fecal samples can be oven-dried (60°) to provide rapid analysis and yield accurate results for concentration of nitrogen and microhistological botanical composition. Oven drying reduced the sample preparation time compared to freeze drying. Fecal samples should be collected as soon as possible following defecation. However, the nitrogen concentration and the percentage of identifiable characteristics in most major plant categories were not affected by exposure through 72 hours in winter and 24 hours in the summer. Bleach in the blending medium reduced the effect of pigment masking and increased the proportion of identifiable epidermal cells. The percentage identifiable fragments in feces was significantly reduced when cattle were grazing dormant and weathered forage during winter compared to samples collected during the summer.

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Economic optimum big sagebrush control for increasing crested wheatgrass production

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Abstract

An approach was developed for estimating the economic optimum rate of initial overstory kill for increasing seasonal forage availability. The model was formulated using: (1) a biological production function relating understory production to initial kill percentage, (2) a derived demand function for seasonal forage value, and (3) a cost of overstory kill function for each control method. The specific optimum solution will vary with the situation; however, the general model may be applied to any ranching situation where understory forage production is constrained by undesirable overstory vegetation. The model was illustrated using the big sagebrush—crested wheatgrass vegetation type on a Utah cow-calf-yearling operation with prescribed burning, 2,4-D spraying, and tebuthiuron application as control methods. For the ranch analyzed, a big sagebrush kill rate between 92 and 100% is optimal depending on the derived demand and cost-of-kill functions used. Kill rates that differ from the optimum caused significant opportunity costs to be incurred.

Key Words: optimization, overstory control, understory release, economics

Investments in control of undesirable vegetation to increase forage production have the potential to increase red meat production, ranch profits, and other benefits to society such as reduced soil erosion. To achieve such benefits requires careful planning, implementation, and monitoring of vegetation control projects. The purpose of this study was to investigate and develop usable mathematical and tabular approaches for estimating the optimum (profit maximizing) rate of initial overstory kill for increasing seasonal forage availability on a given ranch. The focus is how the ranch should approach biological and economic decisions for the alleviation of an identified seasonal forage bottleneck in a yearlong ranch operation.

The biological relationship between overstory dominance and understory production has been documented for many vegetation types (Ffolliott and Clary 1982, Bartlett and Betters 1983). The analytical approach examined in this study was illustrated using big sagebrush (*Artemisia tridentata* Nutt.)—crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult., *A. cristatum* (L.) Gaertn.) vegetation relationships in a Utah cow-calf-yearling operation. The rate of big sagebrush re-establishment on a specific site depends on the percentage initial kill, subsequent grazing management, ecological adaptation of sagebrush to the site, and reinvasion of sagebrush from outside the treatment area (Pechanec et al. 1965, Hull and Klomp 1966, Johnson and Payne 1968, Winward 1983). Benefits from brush reduction include improved range condition, increased forage and livestock production, ease of working cattle, increased feed for wildlife, and improved watershed conditions (McDaniel 1980). Multiple use management may dictate that not all big sagebrush be removed. However, Evans et al. (1979) examined the biological relationships and recommended complete reduction on some areas and no treatment on adjacent areas. The approach described in this paper should be applicable in any vegetation type exhibiting an undesirable overstory-desirable understory relationship and for any ranch operating year-long subject to seasonal forage shortages.

Methods

Production Function

The response of established crested wheatgrass to big sagebrush reduction has been studied on both basin big sagebrush (*A.t.* subsp. *tridentata* Nutt.) and Wyoming big sagebrush (*A.t.* subsp. *wyomingensis* Beetle) sites in southern Idaho (Hull and Klomp 1974). Big sagebrush was reduced 0, 50, 75, and 100% from initial canopy covers of 33.7 and 11.4% at the basin and Wyoming sites, respectively, with initial densities of about 20 plants per 100 ft^2 (9.29 m^2). Burning, 2,4-D, and hand grubbing were used at each kill level in 2 blocks at each site (near Twin Falls and Holbrook, Idaho). Crested wheatgrass response was not significantly affected by treatment method. The important factor was the amount of big sagebrush removed. Killing the last 25% of the big sagebrush stand resulted in 135 and 98% more grass than killing the first 75% on the basin and Wyoming big sagebrush sites, respectively (Hull and Klomp 1974).

Data from the basin big sagebrush and Wyoming big sagebrush sites were analyzed separately to estimate 2 specific production functions. Multiple regression was used to estimate the production function using the computer econometric program "SHAZAM" (White 1978). A 2-year deferment (treatment year and year following) was assumed and the function was estimated using data from 1967 to 1970, inclusive. Crop year precipitation and crested wheatgrass stand age were used in the estimation procedure as suggested by Sneva and Britton (1983) and White (1985). The production function was based on the assumption that any increase in forage from an overstory treatment remained constant from the first year of grazing until the end of the project life. Maximum project life was defined as the time interval required for big sagebrush canopy cover on the treated area to equal its pretreatment level.

The Goodness-of-Fit Test ($\alpha = 0.05$) and the coefficient of skewness test were used to assess normality as described by Kmenta (1971). If these 2 tests disagreed, the scatter plot of residuals was examined and a judgment made about the effects of any departure from a normal distribution on model estimation and interpretation. The test statistic, $\hat{\lambda}$, as described by Kmenta (1971) was used to test for homoskedasticity using the 4 sample points. The 4 years of data used to estimate the function were tested for autocorrelation by use of the Durbin-Watson test as described by Kmenta (1971). Degree of multicollinearity was determined by (1) an examination of the correlation matrix of coefficients and (2) by the "R^2-delete" method (Kmenta 1971).

The overall production function significance was tested with the F-test ($\alpha = 0.05$) and individual coefficients with the Student's *t*-test. The formal criteria for including a variable in the final model were: (1) whether the *t*-value for a coefficient was statistically significant or (2) whether the computed *t*-value was greater than one when the computed *F*-value was statistically significant in order to maximize the value of the adjusted R^2 (Kmenta 1971). Statistically significant environmental and time variables were set

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at their respective long-term average values for the area and added to the regression constant. The resulting deterministic production function related initial big sagebrush kill levels to "typical" or average crested wheatgrass production.

Production function values were adjusted for both desired utilization rate and availability of forage to livestock. The availability function was based on observations by Hull and Klomp (1974) and assumed to be linear between 40 and 90% as big sagebrush canopy cover varied from 34 to 0%. The last 10% unavailable was assumed to be due to the inability of a method to remove all sagebrush skeletons so that some obstacles to forage availability remained. The optimum utilization rate of crested wheatgrass by grazing herbivores was set at 65% (Torell 1984).

Derived Demand for Spring Forage

The "typical" Utah ranch operation data set was analyzed by the COPLAN linear programming (LP) model (Evans 1978) to identify the value of additional crested wheatgrass forage obtained by reducing big sagebrush canopy cover on a given ranch with a given mix of forage sources. The "typical" Utah ranch with 206 brood cows operates as a cow-calf-yearling operation with a 15% replacement rate, a 24:1 cows bred:bull ratio, and an 82% calf crop based on January 1 inventory of brood cows (Dickie and Workman 1985). Feed sources include native foothill range, crested wheatgrass on treated established stands, meadows, crop aftermath, and forage available through Bureau of Land Management permits, U.S. Forest Service permits, and private leases. Additional spring forage has been identified as a need and one option for providing it was to reduce big sagebrush to increase early maturing grasses. Demand for this additional forage is derived from the underlying production process (hence the term derived demand). Demand is defined in economics as the amount of a good or service that a buyer is willing and able to buy at any given price, all else equal. Derived demand for additional early spring forage represents the amount that a given ranch is willing and able to spend for that forage, all else equal (e.g., variable costs of production, livestock prices, other forage sources, livestock enterprise).

Each forage production level of treated crested wheatgrass pasture was used in COPLAN with all other forage sources constant (except untreated hectares of crested wheatgrass were reduced by the size of the treated stand). Each run resulted in a different shadow price ($/ha) for crested wheatgrass forage. The crested wheatgrass forage shadow price represented the net value to the ranch of 1 additional acre of crested wheatgrass. This shadow price was converted to a $/kg value by dividing by the corresponding production per ha value. A derived demand function (relating price of crested wheatgrass forage to usable forage produced) for additional crested wheatgrass production was estimated from the results and used in the optimal kill models.

Valuation of additional forage was based on the premise that no 2 ranches are alike. The fixed cost per kg of forage produced was between $0.003/kg and 0.006/kg for the "typical" Utah ranch studied by Capps and Workman (1982). A rounded average value of $0.0045/kg was subtracted from the short-term function to yield a long-term derived demand function. Short-term was based on the time frame where some of the costs of production do not change with the level of production and as such do not enter into the optimization model. In the long-term, however, the ranch must account for these costs in order to stay in business. The long-term derived demand function was used to show this effect on profits.

Cost-of-Kill Functions

Cost-of-kill functions were designed to predict cost per hectare for any given level of initial big sagebrush kill in a wide geographic area. On-the-ground average costs for prescribed burning, 2,4-D spraying, and tebuthiuron application were obtained from interviews conducted with range conservationists with the Bureau of Land Management (Salt Lake City, Utah, and Boise, Idaho), U.S. Forest Service (Malad, Idaho), and Soil Conservation Service (Tremonton, Logan, and Price, Utah) on specific big sagebrush reduction projects conducted between 1980 and 1984. Data were collected for initial kill percentage, project size, actual investment (i.e., total and per hectare project costs), big sagebrush subspecies, type of treatment, pretreatment big sagebrush canopy cover, and estimated precipitation zone. The latter information was used to identify projects with similar conditions to increase the homogeneity of the data set used.

Additional control efforts were always required to achieve 100% kill of a stand of big sagebrush. No single method was completely effective. It was assumed that each of the 3 basic methods was used at its most efficient level (giving the highest obtainable kill) and then the additional follow-up cost for complete reduction was added to obtain the cost for 100% kill. A $10/ha charge was added to the highest observed percent kill level cost/ha to estimate costs of complete kill based on values published in the literature for individual plant burning or hand grubbing (Arnold et al. 1964).

Optimization Procedure

The objective function for the optimum kill model was equivalent to the formula commonly used in present net worth (PNW) analysis of range improvement practices (Workman 1981). The usable forage per hectare was multiplied by the shadow price appropriate for the initial kill level to determine the annual net benefit of the project to the specific ranch. Each annual net benefit was discounted to the present and summed to obtain the present net value of project benefits per hectare. Project costs (initial per hectare investment) for each particular combination of initial kill and project size were estimated and subtracted from the project benefits to estimate PNW. The optimization model was used to determine the profit maximizing initial kill level.

PNW was then calculated in a "typical ranch" context, based on the estimated functions. The basin and Wyoming big sagebrush-crested wheatgrass production functions were each combined with short- and long-term annual net value and cost of kill functions for prescribed burning, 2,4-D spraying, and tebuthiuron application. The long-term annual net value included the fixed costs allocated to the project on a per hectare basis (Torell 1984). The discount rate of 7% used in the analysis consisted of a real rate of 4% and a risk factor of 3% (Torell 1984).

The tabular approach was used to find a quasi-optimal solution using an electronic spreadsheet (Lotus 1-2-3™) following tabular solutions illustrated by Workman (1986). Annual usable forage values were multiplied by the short-term crested wheatgrass value function with the resulting annual net benefit values. Present net benefits (PNB) for each initial kill level were then computed as the present value of project benefits minus present value of benefits without the project. Present net worth estimates were calculated for each initial kill alternative by subtracting initial investment from PNB.

Results and Discussion

The model was developed under the premise that the spring grazing season constrains the year-long grazing cycle and that the shortage of early spring forage had resulted from the decline in an existing forage stand. Once the need for additional forage was identified, the manager must compare the value of additional forage to the costs of obtaining that additional forage from an overstory reduction project.

Theoretical Model

The objective function is to maximize PNW from additional crested wheatgrass forage over the life of the control project. The production function, cost-of-kill function, and the value of additional crested wheatgrass function are combined to form the optimization model. The model assumes (1) constant deferment periods among treatment intensities, (2) a given grazing management strategy, (3) that the treatment method does not affect biological responses except through the level of initial kill, and (4) that the crested wheatgrass stand is subject to big sagebrush re-establishment.

The optimization model is stated as

$$\max_{X,\ \bar{S}} N(1) = \sum_{t=t_o}^{\bar{S}} P\,[U\,A\,Y]e^{-\rho t} - K \qquad (1)$$

where

N(1) = Present net worth of a single treatment period per ha (\$/ha),
Y = Average crested wheatgrass production function for a given $\bar{S}$ (kg/ha),
X = Initial kill level of big sagebrush (% canopy reduction),
K = Cost of initial kill function (\$/ha),
P = Derived demand function for crested wheatgrass forage (\$/ha),
U = Utilization rate (%),
A = Crested wheatgrass availability function (%),
t = Stand age since last treatment (integer years),
t_o = First post-deferment grazing period,
$\bar{S}$ = Maximum project life for a given initial kill level,
ρ = The discount rate.

In addition, the problem is defined such that initial big sagebrush canopy cover is not more than 34% and the desired AUM increase, season of use, livestock class, and grazing system are specified. Eq. (1) represents an unconstrained maximization problem where the objective is to maximize the PNW of a project with respect to the choice of X and $\bar{S}$. Note that in the deterministic model given here, once X is selected, $\bar{S}$ automatically follows by assumption. The first-order conditions for optimization specify that at the optimum point (1) the change in the discounted accumulated annual net returns must equal the change in the cost of the kill function when both are evaluated at X* (the solution value of X) and (2) that at $\bar{S}$*—the maximum project life associated with X*—no further gains can be made by extending project life another year.

Empirical Model Estimation

Coefficients for each function are given in Table 1. The overall equations were significant based on the F-test. The production functions shown in Figure 1 were set at average year values. Production of crested wheatgrass was multiplied by utilization and availability factors to convert it to usable forage produced. The resulting equation was:

$$\begin{aligned}\Phi &= U\,A\,Y = 0.65\,(0.4 + 0.005\,X)\,Y \\ &= (0.26 + 0.00325\,X)\,Y \qquad (2)\end{aligned}$$

where Φ = Usable crested wheatgrass forage (kg/ha), and all other variables are defined as in Eq. 1.

The forage valuation approach allowed COPLAN to select the best available forage alternative (e.g., native foothill range, untreated crested wheatgrass stands, leases and permits) given a specified level of treated sagebrush in an existing crested wheatgrass stand. The valuation method also emphasized the economic principle that when an input is in oversupply (i.e., nonconstraining), an additional unit has no value to the ranch. The short-term

Table 1. Production, derived demand, and cost-of-kill function coefficients with estimated t-values in parentheses. Adjusted R^2 and F-values for each equation are shown below the coefficients.

	Production		Demand	Cost-of-Kill			
	Basin ln (Y+1) (kg/ha)	Wyoming ln (Y+1) (kg/ha)	Net Value (\$/kg)	Burn 1 Kbl (\$/ha)	Burn 2 Kb2 (\$/ha)	2,4-D ln(Ks+1) (\$/ha)	Tebuthiuron ln(Kt+1) (\$/ha)
Int	5.853	13.022	0.053	4.007	9.774	3.290	2.027
	(58.44)	(21.48)	(15.85)	(0.39)	(2.05)	(13.10)	(7.78)
X1		2.27E-03		1.036	0.244	0.018	0.052
		(1.86)		(1.24)	(4.39)	(1.15)	(3.41)
X2	1.09E-04	3.85E-05		-1.76E-02		-6.68E-04	-1.05E-03
	(22.19)	(3.66)		(-1.07)		(-2.15)	(-4.03)
X3				1.06E-04		5.25E-06	7.47E-06
				(1.14)		(2.87)	(5.55)
X4	0.306	-6.297					
	(1.99)	(10.85)					
X5		1.716					
		(9.84)					
X6		-0.142					
		(-8.59)					
X7	0.316						
	(8.01)						
X8				-0.056	-0.056		
				(-4.41)	(-4.72)		
X9				3.65E-05	3.75E-05		
				(3.79)	(4.10)		
X10			-2.88E-05				
			(-5.32)				
R^2	0.94	0.97	0.77	0.61	0.61	0.54	0.98
F	188.26	225.65	28.33	8.24	8.24	12.53	485.95

Where
X1 = Initial big sagebrush kill (%)
X2 = Initial big sagebrush kill squared
X3 = Initial big sagebrush kill cubed
X4 = Time after treatment (years)
X5 = Time squared
X6 = Time cubed
X7 = March precipitation (inches)
X8 = Project size (treated ha)
X9 = Project size squared
X10 = Usable forage (kg/ha)

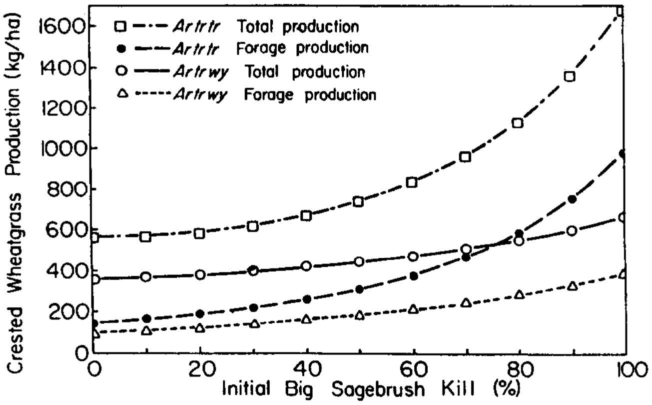

Fig. 1. *Crested wheatgrass production and forage yields as functions of percentage kill of 2 big sagebrush subspecies.*

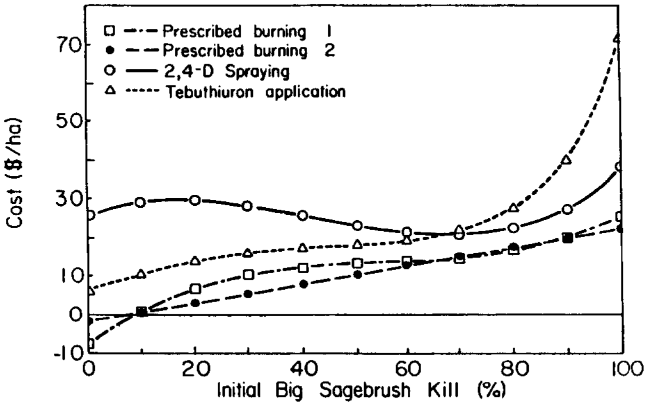

Fig. 2. *Big sagebrush control costs as functions of percentage kill, 4 control methods.*

derived demand coefficients are given in Table 1. This procedure understates the total value of the forage to the ranch by the area under the derived demand curve and above the annual value selected (i.e., consumer surplus). In essence, all of the forage produced is valued at the marginal value. Once the usable forage level is determined, a forage price is specified. As with any deterministic model, use of LP can only approximate real world situations.

The costs-of-kill function coefficients are given in Table 1 and graphed in Figure 2. Of the estimated functions, only the prescribed burning (Kb2) cost was linearly related to initial kill level and all other functions were sigmoid (Fig. 2). Of the nonlinear functions, the 2,4-D (Ks) function did not appear to "fit" preconceived ideas of functional shape—i.e., zero % kill had a significant cost and costs at low kill levels were greater than at higher kill levels. The prescribed burning (Kb1) and tebuthiuron application (Kt) cost of kill functions more accurately depicted the expected relationship. Project size (i.e., treated ha) was retained only for the prescribed burning function. No such effect was found for 2,4-D, and the effect was deemed insignificant for tebuthiuron projects. The cost-of-kill approach employed in this study considers the type of method to use and how intensively that method is used.

The annual net return function is obtained by multiplying either

Table 2. Solution to the optimal basin big sagebrush kill level using the short-term derived demand and tebuthiuron cost of kill function.

Initial kill (%)	Annual usable forage (kg/ha)	Annual net return ($/ha)	Project life (yr)	PNB ($/ha)	Initial cost ($/ha)	PNW ($/ha)
0	146	7.15	0	−13.83	6.59	−20.42
10	166	8.03	5	−11.02	10.60	−21.62
20	191	9.09	6	−6.39	14.04	−20.43
30	222	10.36	7	0.49	16.31	−15.82
40	261	11.91	8	10.14	17.50	−7.35
50	312	13.77	10	26.52	18.18	8.34
60	379	16.00	12	48.20	19.19	29.00
70	468	18.56	14	75.28	21.57	53.71
80	589	21.28	16	106.48	27.02	79.46
90	753	23.66	18	136.83	39.39	97.44
100	982	24.37	25	170.82	69.72	101.10
80	589	21.28	16	106.48	27.02	79.46
81	603	21.55	16	108.75	27.85	80.90
82	618	21.81	16	110.99	28.74	82.24
83	633	22.07	16	113.19	29.72	83.47
84	648	22.32	16	115.34	30.78	84.56
85	664	22.57	16	117.44	31.93	85.51
86	681	22.81	17	124.43	33.17	91.25
87	698	23.04	17	126.46	34.53	91.92
88	716	23.26	17	128.39	36.02	92.38
89	734	23.46	17	130.23	37.63	92.60
90	753	23.66	18	136.83	39.39	97.44
91	773	23.84	18	138.46	41.31	97.15
92	793	24.00	19	144.60	43.42	101.18
93	814	24.14	19	145.94	45.72	100.22
94	836	24.26	20	151.49	48.24	103.25
95	858	24.36	20	152.43	51.02	101.41
96	881	24.43	21	157.27	54.06	103.21
97	905	24.47	22	161.58	57.42	104.16
98	930	24.47	23	165.30	61.11	104.18
99	955	24.44	24	168.39	65.20	103.19
100	982	24.37	25	170.82	69.72	101.10

the short-term or long-term derived demand function by the usable forage function (Eq. 2) such that:

$$\begin{aligned} D_s &= P\ U\ A\ Y = P\ \Phi \\ &= (0.053 - 0.000028\ \Phi)\ \Phi \\ &= 0.053\ \Phi - 0.0000228\ \Phi^2 \end{aligned} \tag{3}$$

and similarly

$$D_l = 0.048\ \Phi\ 0.0000228\ \Phi^2 \tag{4}$$

where D_s = Short-term annual net return function (\$/ha),
D_l = Long-term annual net return function (\$/ha),
and P, U, A, Y, Φ, and X as defined in Eqs. (1) and (2).

Equations 3 and 4 provide the components of the optimization model established in Eq. 1 over which the ranch can exercise some control in its decision-making process. Once an initial kill level is determined, the value of D_s and D_l are also determined for the relevant project life. The difference in the 2 equation intercept terms is due to the fixed cost allocation in the long-term function.

Any of the cost of kill functions can be combined with Eq. 3 or Eq. 4 to estimate an optimal target kill rate. The discounting factor is the final model component. This factor requires 3 variables—the discount rate (ρ), deferment length (t_o), and maximum project life ($\bar{S}$). The total mathematical optimization model is written using the basin big sagebrush production function, short-term derived demand function, and tebuthiuron cost-of-kill function as:

$$\begin{aligned} N(l) = &\sum_{t=t_o}^{\bar{S}} (0.053\ \Phi\ 0.0000288\ \Phi)e^{-0.07t} \\ &-(\exp(2.027 + 0.052\ X - 0.00105\ X^2 \\ &+ 0.00000747\ X^3) - 1 \end{aligned} \tag{5}$$

The last part of this equation is the tebuthiuron cost-of-kill function solved for Kt (see Table 1). The first order condition for a maximum of this model is not easily solvable to find the profit maximizing level of initial kill (X*).

Utah Application

A convex (bowed downwards) production function as illustrated in Figure 1 has been observed in numerous vegetation types ranging from semidesert to forest. Given a constant cost of kill and constant forage value as normally assumed, a convex production function always implies an optimal solution with an overstory kill of either zero or 100%. Addition of the derived demand and cost of kill functions prevents this automatic (and overly simplified) conclusion.

The tabular solution to Eq. 5 is shown in Table 2 for given initial kill rates. The results shown in Table 2 indicate that the optimal (profit maximizing) kill level lies between 80 and 100%. The lower portion of Table 2 shows the PNW estimates for each integer kill level over this 20% range. For this procedure the optimal target kill rate is about 98%, which is expected to return \$104.18 per ha over the 23-year project life.

The opportunity cost associated with a non-optimal target kill rate may be substantial. Investments in overstory kill resulting in a non-optimal kill level would result in lower profits than shown in Table 2. For example, if a decision is made to kill only 50% of the basin big sagebrush in an area (perhaps to produce forage for livestock and to maintain cover for wildlife) rather than the optimum kill rate, the ranch will incur an opportunity cost of about \$104/ha and will receive only about \$8/ha, a foregone net benefit of about \$96/ha. To produce the same amount of additional forage, it would be necessary to treat more than 3 times as much land. In addition, the treated land would not result in a profit maximizing solution.

All other combinations of big sagebrush subspecies, derived demand, and kill methods were analyzed (Table 3). In all cases tested, results indicate the optimal kill rate lies between 92 and 100%. The highest PNW estimates were for burning, followed closely by 2,4-D spraying. All optimal initial kill levels shown in Table 3 are sensitive to the utilization rate and discount rate assumptions used in their derivations. The tebuthiuron results illustrate 2 economic points: (1) the lower long-term forage value (due to a fixed cost allocation) caused the optimal initial kill value to decline and (2) the lower productivity (and smaller response) of the Wyoming big sagebrush site resulted in lower PNW estimates. The prescribed burning results illustrate a third point: when project size increased, the cost of kill function was shifted vertically downward such that at a given initial kill level the curve slopes were about equal. Results shown in Table 3 indicate that this shift did not affect the optimal kill rate but did increase project PNW.

The points illustrated by Table 3 agree with general economic theory: (1) as the price of an output decreases, less of the variable input should be used to produce it; (2) invest in the best opportunities (more productive sites) first; (3) corner solutions (i.e., 0 or 100% kill) such as found with 2,4-D spraying of Wyoming big sagebrush are relatively insensitive to price changes; and (4) that the optimal solution depends on the slope of the functions rather than their absolute values. Because of the discrete time aspect of the problem, PNW values tended to change discontinously as seen

Table 3. Summary of optimal target kill rates for combinations of big sagebrush subspecies production, derived demand, and cost of kill functions for the STP static model.

	Basin big sagebrush				Wyoming big sagebrush			
Method	Short-term		Long-term		Short-term		Long-term	
Tebuthiuron								
Initial kill (%)	98		92		99		92	
Investment (\$/ha)	61		43		65		43	
PNW (\$/ha)	104		68		46		29	
2,4-D Spraying								
Initial kill (%)	100		98		100		100	
Investment (\$/ha)	39		35		39		39	
PNW (\$/ha)	132		87		76		57	
	50 ha	150 ha	50 ha	150 ha	50 ha	150 ha	50 ha	150 ha
Burning (Eq. 1)								
Initial kill (%)	100	100	99	99	100	100	100	100
Investment (\$/ha)	34	30	34	29	34	30	34	30
PNW (\$/ha)	137	141	89	94	81	85	62	66
Burning (Eq. 2)								
Initial kill (%)	100	100	100	100	100	100	100	100
Investment (\$/ha)	31	26	31	27	31	26	31	27
PNW (\$/ha)	140	145	92	96	84	89	65	69

in the last column of Table 2.

An assumption used in developing the cost-of-kill functions was to add $10/ha to the cost of producing the highest kill rate for each treatment. Although this assumption was not critical to the analysis, it was added to make the situation somewhat more realistic. It was felt that to achieve 100% kill would require additional investments (i.e., it could not be done for free). As with any assumption, its value or direction could be changed and the analysis redone to account for this. In fact, this should be done when applying the model to any actual ranch situation.

From an economic efficiency or profit view for this particular ranch, an overstory kill project should be implemented to achieve the highest possible initial kill level. On better (more productive) sites, the goal may not be complete control since the same level of PNW could be achieved for less investment. Nevertheless, kill rates in excess of 90% require skillful application of the method under nearly ideal conditions. A threshold initial kill level likely exists for each method (where PNW goes from negative to positive as higher initial kill levels are achieved), as illustrated in Table 2 between 40 and 50% initial kill. The extreme solution would be when this transition occurred at either 0 to 100% kill.

Conclusions

The analytical process described will help identify and define components necessary for an optimization process and for ranch planning. However, more information is needed about long-term biological production relationships over a wide variety of conditions in different vegetation types, e.g., the effects of overstory reestablishment and grazing management on the time path of forage production following overstory kill. More accurate information will increase the feasibility of dynamic (time effects considered) model formulation for on-the-ground management decisions. Cost-of-kill relationships for each method must also be more accurately defined. Ideally, costs to achieve a target kill rate should be predictable for a specific area, taking into account differences in costs due to topography, rockiness, and stand density. The resulting models would be more realistic in terms of economic and biological relationships.

The analytical models developed in this study demonstrate the potential rewards of well-planned and well-managed forage stands that are susceptible to undesirable overstory re-establishment. The model provides estimates of project PNW, the optimal investment level, and required project size. The 2 estimable functions (production and cost of kill) can be developed independent of information of a specific ranch required in the planning process. However, the optimization procedure requires that the total ranch effects of a change in seasonal forage availability be identified. The year-long operation of a ranch must be identified and described quantitatively, both biologically and economically. This information is required for ranch planning in general.

Although ranchers may not be prepared to use a linear programming model to generate forage shadow prices, the method is available and useful. Some producers currently use LP while others have access to the COPLAN model through the SCS and private consultants. It may also be feasible to substitute other simpler forage valuation techniques with the recognition that there will be a loss in accuracy. No matter what valuation method is used, it must use feasible forage alternatives for the forage bottleneck season and value that forage as such.

The model can be implemented with existing data bases and ranch information. This is not to suggest that the information is easily obtained and analyzed, rather that is obtainable in a reasonable time frame on a specific ranch basis. The move from a static (i.e., time is not a factor) to a dynamic production function represents a biological step toward realism, while the move to an optimal control model (as described in Kamien and Schwartz 1982) is the next economic step. The "no data" problem discussed by Torell (1984), Martin (1972), and Burt (1972) in long-term dynamic optimization models does not appear to be a significant problem with the developed model. Enough research results are available to reasonably estimate static production functions. Data for estimating dynamic production functions are more difficult to obtain by standard rangeland inventory procedures except in short-lived projects such as those described by Ethridge et al. (1984) and economically analyzed by Torell and McDaniel (1986). Otherwise, long-term biological production data sets must be provided through a simulation model.

The developed optimization model is obviously less realistic than the dynamic models described by Cotner (1963), Burt (1971), and Torell (1984). It does, however, have the advantage of reasonable data requirements while at the same time capturing many of the complexities of the optimization problem. As Burt (1982) stated, "the primary objective in all modeling is to capture the essential aspects ... yet keep the model as simple as possible." The developed model appears to hold promise for fulfilling this requirement in applied planning. This agrees with Martin's (1972) conclusion that the range profession has not yet provided adequate data bases for the empirical solution of dynamic optimization models. As pointed out by Burt (1972), one benefit of economic modeling is to define the requisite relationships for analysis. One goal of this project was to further develop these relationships.

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An economic assessment of risk and returns from prescribed burning on tallgrass prairie

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Abstract

A stochastic (Monte Carlo) simulation model was developed to evaluate the influence of prescribed burning on the expected value and variability of net returns from a representative stocker cattle enterprise. The model was applied to both shallow prairie and eroded prairie range sites in eastern Oklahoma. Prescribed burning is shown to be an economically feasible means of improving the productivity of eastern redcedar infested rangeland. Implementation of an annual burning program resulted in a $69.00 and $4.80 per hectare increase in the net present value of the 10-year return stream generated from stocker cattle production on shallow prairie and eroded prairie range sites, respectively. Prescribed burning does not increase the variability of annual income from stocker cattle production. However, when risk is measured in terms of relative variability (coefficient of variation) or the probability of annual returns below zero, prescribed burning is determined to be a risk-reducing practice.

Key Words: plant control, eastern redcedar *Juniperus virginiana*, range improvements, stochastic simulation model, profitability, risk, variability of returns

Maintenance and improvement of the productivity of Oklahoma's rangeland is critical to the long-run profitability of the state's beef cattle industry. Considerable concern has been expressed by decision makers and agriculturalists as to the declining condition and productivity of Oklahoma's range resource. Recent estimates indicate that forage production has been reduced below 50% of potential on 70% of Oklahoma's rangeland. Also, forage production on over 4 million of Oklahoma's 6.3 million hectares (65%) of rangeland could be increased by some form of brush control (Soil Conservation Service 1982).

Much of the decline in the condition of Oklahoma's rangeland may be attributed to the reduced profitability of cattle enterprises and its depressing effect on incentives to invest in range improvements. Implementation of most brush control practices requires substantial initial investment followed by increased annual benefits experienced several years into the future. Many producers' financial position precludes them from incurring the negative influence of these investments on initial annual cash flows. Range improvement practices are needed that require low initial investment and provide immediate benefit in the form of improved animal performance or production.

Prescribed burning has been advocated as a profitable range improvement practice under the economic environment currently faced by livestock producers. The most appealing feature of late-spring burning is that it provides immediate benefits in the form of increased stocker cattle weight gains (Anderson et al. 1970, Owensby and Smith 1979). These short-term benefits result from improvements in the quality of forage available to grazing cattle (Allen et al. 1976). Data from Kansas (Anderson et al. 1970, Owensby and Smith 1979, and Woolfolk et al. 1975) and Oklahoma (McCollum 1987) indicate that summer gains of yearling cattle on tallgrass prairie increase 10 to 20% in response to prescribed burning. Burning also provides long-term range improvement by advancing grassland succession and favoring desirable grasses (Anderson et. al. 1970, McMurphy and Anderson 1965, and Towne and Owensby 1984) and controlling undesirable weed and brush species, especially eastern redcedar (Anderson et al. 1970, Stritzke et al. 1975, and Stritzke and Rollins 1984). Thus, prescribed burning offers the producer an opportunity to meet the long-term goals of income stability, increased net worth, and improved range condition without incurring significant negative cash flows in the initial portion of the planning horizon. Of course, prescribed burning is not without its disadvantages. Reductions in soil moisture as a result of burning can decrease forage yield in dry years (Anderson et al. 1970). In addition, improper timing of prescribed burns and poor grazing practices on burned rangeland can have considerable detrimental effects (Towne and Owensby 1984, Anderson et al. 1970).

Economic analysis of range improvement investments has traditionally been conducted through application of net present value (NPV) criteria in a partial budgeting framework. Annual cash flows (income less costs) are estimated over the investment's life, discounted by an appropriate discount rate, then summed to determine the NPV of the investment. The NPV estimates may then be used to estimate the profitability of an investment or rank alternative investments. Previous applications of this approach

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include Whitson and Scifres 1981, McBryde et al. 1984, Garoian et al. 1984, and Scifres 1985. Cotner (1963) and Jameson (1971) employed a variation of this discounting approach to determine optimum timing of range improvement controls.

The primary shortcoming of these analyses is that they are deterministic, ignoring the uncertainty inherent in livestock production and the effect of this uncertainty on the economic feasibility on the range investment. Production response is based upon expected forage and animal response to the range improvement practice. Also, product prices and factor costs are set at predetermined levels. When evaluating range investments, consideration must be given to the effect of adoption on risk (income variability) as well as expected income levels. Range improvement practices that increase risk along with expected income may not necessarily be production techniques preferred by the rancher. Thus, criteria based upon income variability as well as profitability measures should be employed to evaluate the efficacy of range investments (Cook and Stubbendieck 1986).

A second shortcoming of range investment analyses conducted using a partial budgeting framework is their failure to fully represent the economic consequences associated with a range improvement program. The influence of a negative annual cash flow not only affects the NPV of income in the current year, but also reduces income in future years if additional debt is incurred to cover operating losses. A whole-ranch approach must be employed to accurately measure the economic ramifications of a particular range improvement investment.

The objective of this study is to evaluate the influence of prescribed burning on both the expected value and variability of net returns from a representative stocker enterprise. Economic evaluations of a burning program on shallow prairie and eroded prairie range sites are reported.

Methods and Procedures

Model Description

To represent the effect of prescribed burning in an uncertain production and economic environment, a stochastic (Monte Carlo) simulation model was employed. Monte Carlo models have been advocated as a useful means of exploring alternative investment strategies and their uncertain consequences (Anderson et al. 1980). Monte Carlo simulation involves the mathematical representation of a system, wherein critical stochastic variables are represented using specified probability distributions. In economic applications, important product prices, costs, and yield are typically specified as stochastic variables. Random variables drawn from these distributions are used in the model to simulate the firm's performance. By repeating this procedure many times, probability distributions of important economic performance measures can be derived.

The simulation model used in this study was developed to represent the production, marketing, and financial aspects of a representative ranch over a 1-year planning horizon. The model includes several stochastic factor cost, output price, and livestock response variable to represent the uncertainty inherent in stocker cattle enterprises. Through repeated iterations of the simulation model, the effect of various range improvement practices (e.g., prescribed burning) on both the expected value and variability of ranch income may be obtained.

To simulate the representative ranch operation, the model is initialized using a predetermined ranch situation, then run for a 10-year planning horizon following a specified management plan. The initial ranch situation dictates the beginning financial position, range condition, and resource endowments of the representative ranch. At the beginning of each year, steer prices, calf prices, feed prices, and livestock production performance variables are drawn from a multivariate probability distribution. These values are then entered into the model to estimate annual ranch income derived from the specified seasonal management plan. The user-specified management plan stipulates the complete set of production and marketing decisions made by the producer (the number of calves purchased, feed rations, range improvement practices, marketing dates, etc.). The ranch operation is simulated recursively, using the ending financial and resource situation for 1 year as the beginning position for the next.

Alternative range improvement practices may be evaluated using the ranch simulation model by programming the particular practice into the specified production plan. For example, in evaluating the adoption of a prescribed burning program, probability distributions and relationships defining animal performance and range productivity in response to late-spring burning are specified. Also, additional costs of burning are included in the simulation model. The model is run for several iterations to derive distributions of relevant economic variables to be used in evaluating the range improvement investment. The economic consequences associated with prescribed burning may then be determined by comparing these results with those derived under baseline conditions (without prescribed burning). The model may also be under deterministic (no-risk) conditions by fixing each stochastic variable at its expected value. Comparison of the results derived using the stochastic and deterministic specifications indicate the effect of incorporating risk in the range investment analysis.

Production Response

Production data included in this analysis were restricted to those specific yield changes that affect the quantity of marketable product (beef). These include long-run changes in stocking rate associated with adopting (or failing to adopt) a burning program, as well as changes in forage quality that alter the expected value and variability of annual weight gains.

Herbage availability was estimated from Soil Conservation Service Technical Guide[1] herbage yield data for tallgrass rangeland of the Central Rolling Red Prairies Land Resource Area, Payne County, Oklahoma. These data were supported by forage standing crop data for the same area (Powell et al. 1982, Rollins et al. 1985, Brummer 1986, and Engle et al. 1987). In the absence of eastern redcedar trees, peak standing crop (i.e., late July to early August standing crop) was set at 3,360 kg/ha (3,000 lb/ac) on shallow prairie and 2,800 kg/ha (2,500 lb/ac) on eroded prairie, the approximate long-term averages as suggested by these clipping data. Initial herbage availability of 2,800 and 2,240 kg/ha (2,500 and (2,000 lb/ac) for shallow prairie and eroded prairie, respectively, reflects reduced herbage standing crop associated with infestations of 198, 2 to 6m (6 to 20 ft), eastern redcedar trees per hectare, which was adapted from the standing crop data provided by Engle et al. (1987).

Forage release, a result of eastern redcedar control with annual spring burning, is estimated to be maximized in 3 years. The greatest proportion of herbage availability increase is assumed to occur with the first annual burn. With no spring burning, herbage availability would linearly decline to about 1,792 and 1,680 kg/ha (1,600 and 1,500 lb/ac) on shallow prairie and eroded prairie sites, respectively, as a result of additional eastern redcedar encroachment. Thus, over the 10-year planning horizon, eastern redcedar population is assumed to increase from about 198 trees/hectare (80 trees/ac) to 568 trees/hectare (230 trees/ac) on the shallow prairie and from 198 to 420 trees/hectare (80 to 170 trees/ac) on the eroded prairie range sites.[2] Estimated herbage availability over the 10-year time horizon is depicted graphically for both shallow and eroded prairies in Figures 1a. and 2a., respectively.

Stocking rate was set by allowing 12.0 kilograms (26.5 pounds) herbage/steer/day for herbage disappearance, the herbage disappearance associated with stocker cattle grazing tallgrass prairie

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[1] U.S.D.A. Soil Conservation Service, Field Office, Stillwater, Oklahoma.

[2] Based upon an average herbage reduction of 13.23 kg (6.0 lbs.) per tree (Engle et al. 1987).

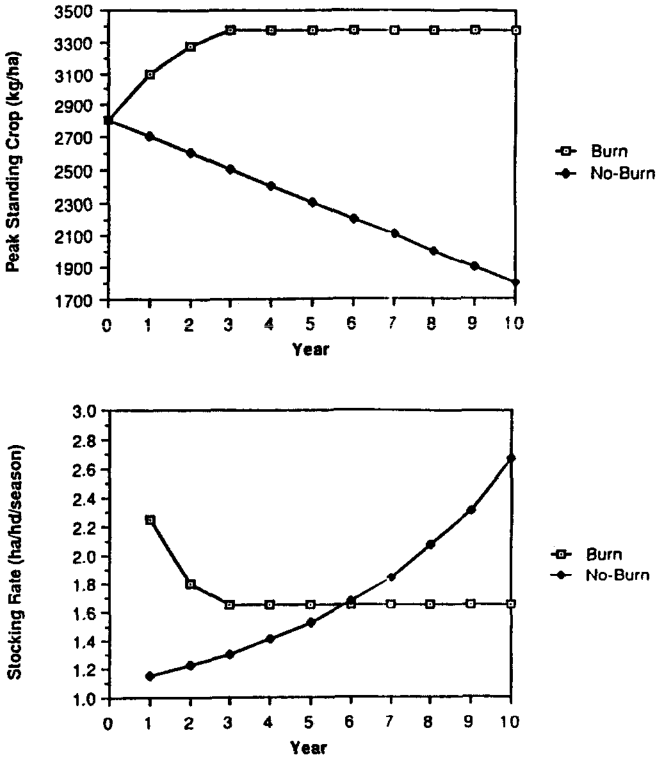

Fig. 1. *Peak standing crop and associated stocking rates for the 10-year time horizon, shallow prairie range site.*

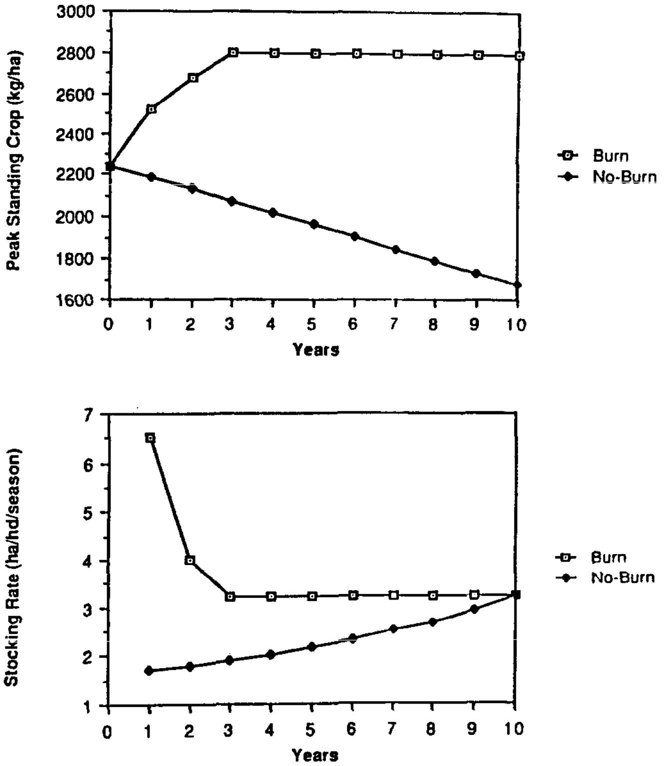

Fig. 2. *Peak standing crop and associated stocking rates for the 10-year time horizon, eroded prairie range site.*

(Brummer 1986). Stockers are grazed from late-April to late-September, a period of approximately 150 days. Herbage allocation on burned pastures was limited to herbage in excess of 2,240 kg/ha (2,000 lb/ac) residue, the fine fuel threshold requirement for late spring burning for eastern redcedar control (Launchbaugh and Owensby 1978, Rollins 1985). On unburned pastures, herbage in excess of 1,120 kg/ha (1,000 lb/ac) was allocated for stocker use. Stocking rates approximate those calculated by Kothmann's (1984) method and the SCS Technical Guide recommended stocking rates, except that stocking rate was set lower on burned pasture to conserve fuel for burning. Our calculated stocking rates on unburned pastures were heavier than Kothmann's in the first portion of the 10-year period to approximate conventional stocking in the region. The derived stocking rates under burn and no-burn conditions for summer stocker production on shallow prairie and eroded prairie range sites are shown in Figures 1b. and 2b.

To represent the short-term effect of prescribed burning, triangular probability distributions of annual steer performance (seasonal weight gain) were derived using late-spring burning from the Kansas Flint Hills and data from Oklahoma State Univeristy (Launchbaugh and Owensby 1978, Owensby and Smith 1979, and McCollum 1987). These distributions reflect the expected value and variability of steer performance resulting from differences in forage quality among years. Prescribed burning is estimated to improve summer gains of yearling cattle an average of 12% on tallgrass prairie in Oklahoma (McCollum). Results reported from several studies investigating the effects of late-spring burning suggest similar improvement in gain from burning (Anderson et al. 1970, Smith and Owensby 1972, Woolfolk et al. 1975, and Owensby and Smith 1979). Mean annual weight gains of 113.4 and 102.1 kilograms (250 and 225 pounds) per steer were specified in the burn and no-burn distributions, respectively. To obtain an estimate of the degree of variability in annual steer gains, a 10-year data set was employed. Since statistical tests indicate no serial correlation, the data were used to estimate the distribution of annual steer weight gains with and without prescribed burning. For reasons cited in Young (1983), 10 and 90 percentiles were substituted for exact endpoints in deriving distribution parameters from the data series. The derived triangular distributions are shown in Figure 3.

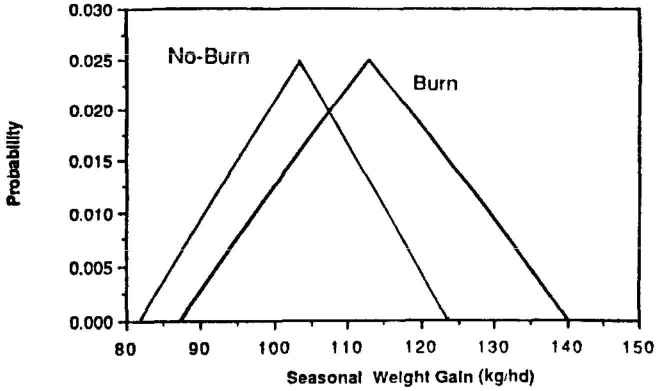

Fig. 3. *Triangular probability distributions of seasonal weight gain on a 216 kg (475 lb) steer, with and without prescribed burning.*

Livestock Receipts and Production Costs

Net returns were determined by combining values derived from the production response models with stochastically derived product price and factor cost estimates. Steer prices, supplemental feed costs (prairie hay and protein supplement), and calf prices were represented using a multivariate normal distribution based upon a historical series of normalized price data. Mean values of distribution variables were determined exogenously from price models that reflect the level of expected values of each price over the time horizon.

Gross livestock receipts were estimated as the product of 3 variables: (1) the number of steers grazed (as dictated by the current stocking rate), (2) the average steer weight (derived from the production model), and (3) the stochastic steer price. Revenues were adjusted to reflect a 2% death loss. Average steer and calf prices were determined from price prediction models specified to represent seasonal and cyclical movements of cattle prices over time.

Annual costs allocated to the stocker enterprise included livestock and non-livestock costs associated with ownership and maintenance of the representative ranch. An itemized list of annual livestock expenses (with stochasic prices set at expected values) is presented in Table 1. Estimated annual costs of pasture burning were estimated to be $5.73 per hectare ($2.32 per acre). Non-livestock expenses included interest and principal payments on short-, and intermediate-term debt, land rental and ownership expenses, property taxes, pasture maintenance and improvement costs, and various ranch overhead expense items. Additional debt may be accumulated over the planning horizon through financing of operating losses.

Table 1. Per head operating cost for stocker steers on eroded prairie and shallow prairie range sites.

Input	Units	Price	Quantity	Value
Steer Calves*	kg	1.59	204	$324.00
Supplemental Feed*	kg	.22	35	7.70
Salt and Minerals	kg	0.77	5.45	4.20
Vet. & Medical Expenses	hd	9.08	1.00	9.08
Mach. Fuel, Lube, & Repairs	hd	5.91	1.00	5.91
Equip. Fuel, Lube, & Repairs	hd	.85	1.00	.85
Hauling Charges*	kg	0.008	544	4.20
Marketing Charges*	kg	0.038	329	12.47
Annual Operating Capital*	dol			26.36
Total Operating Costs				$394.77

*The actual cost of this input is dependent upon stochastic prices or stochastic weight gain values. Costs reported are expected values.

Results and Discussion

The simulation model was applied to investigate the profitability of implementing a prescribed burning program on both shallow prairie and eroded prairie range sites to control eastern redcedar. The profitability of the burning program was estimated by comparing simulation results derived from an enterprise employing late-spring burning each year with baseline results (without prescribed burning).

The current stocker enterprise was assumed to consist of 300 head of stocker steers grazed on 607 hectares (1,500 acres) of tallgrass prairie range. Stocker calves weighing 215.5 kilograms (475 pounds) are purchased in early-April, placed in a 28-day receiving program, and then grazed until late-September (approximately 150 days). Steers are supplemented with 0.45 kilograms (1 pound) of soybean meal per day over the last 77 days of the summer grazing season.

Shallow Prairie Range Site

Expected annual cash flows (receipts less operating costs) from stocker production on a shallow prairie range site were estimated for both burn and no-burn scenarios under stochastic (risk) and deterministic (no-risk) conditions. Annual cash flows from each year of the 10-year planning horizon, accumulated cash flow and the net present value of the cash flows are given for each scenario in Table 2. A real discount rate of 4% was used to estimate the net present value of the 10-year return stream.[3] The risk results represent the expected values of the annual cash flows from 200 itertions of the simulation model. In the deterministic analysis, expected cash flows were estimated using expected values of annual steer performance (weight gain), input cost, and steer price variables.

Results indicated that prescribed burning is an economically feasible range improvement practice for stocker producers operating on shallow prairie range sites. Under stochastic conditions, the net present value (NPV) of the return stream generated using prescribed burning exceeds the no-burn NPV by $41,905 or $69.04 per hectare ($27.94 per acre). Expected returns derived when burning is used exceed no-burn returns for all but the first year of the planning horizon, despite the higher no-burn stocking rate for years 1 through 5 (see Fig. 1b). In years 2 through 5, additional returns derived from improved animal performance on burned pastures exceed returns lost from the lower stocking rate. Returns from prescribed burning increased over the first 3 years of the planning horizon and then appeared to level off. Conversely, returns from no burn scenarios decrease monotonically over time as a result of the declining stocking rate.

Comparison of results derived under risk and no-risk assumptions indicates a decrease in the estimated profitability of stocker production as a result of incorporating stochastic economic and production influences. The NPV of returns derived from deterministic application of the model exceed stochastic estimates for the burn and no-burn scenarios (Table 2). Also, mean annual cash flows from the deterministic analysis exceed annual cash flows for each year of the stochastic analysis. This result primarily reflects 2 conditions. First, because output and factor price variables are not independent, the expected value of net returns under stochastic conditions is not necessarily equivalent to the net return generated using expected price and production values. Also, under stochastic conditions, negative annual cash flows may result from poor animal performance, low steer prices, and/or high factor costs. Financing these operating losses results in an increase in annual operating expenditures relative to those estimated under deterministic assumptions.

Results from the stochastic analysis also indicate the influence of annual prescribed burning on the variability of annual cash flows. Table 2 reports the mean, standard deviation, and coefficient of variation of annual returns for the burn and no-burn scenarios. The standard deviation of annual cash flows increases for 6 of the 10 years of the planning horizon as a result of adopting a prescribed burning program. However, when variability in returns is measured using the coefficient of variation, the variability of returns derived from the no-burn scenario exceeds the variability resulting from using the burning program in 9 of the 10 years. Furthermore, the magnitude of this difference increases over time.

It may be argued that return variability does not accurately reflect the risk inherent in a particular livestock enterprise since both deviations above and below the mean contribute to the estimated level of risk. Several researchers have proposed a "safety-first" risk measure where the degree of risk inherent in an enterprise is measured by the probability of returns falling below some critical level (Walker et al. 1986, Robinson et al. 1984). To illustrate this concept, the probability of annual cash flows falling below zero during each year of the time horizon is given in Figure 4. When a critical return level of zero is assumed, the level of risk in stocker production is reduced in every year as a result of implementing a burning program. The probability of negative annual cash flows is reduced from 5% in year 1 to as much as 26% in year 10.

Eroded Prairie Range Site

Expected annual cash flows for stocker enterprises on eroded prairie range sites are given in Table 3. Under both stochastic and determinist assumptions, the NPV of returns from the burning scenario exceed those derived from the no-burn scenario. This result occurs despite the fact that annual cash flows from stocker production without prescribed burning exceed cash flows from the prescribed burning scenario for the first 3 years of the planning horizon. Higher productivity of burned range sites (and lower productivity of unburned sites) results in increased stocking rates

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[3] All prices and costs employed in the model are expressed in real (non-inflated) terms. Thus, a real discount rate (4%) is employed to represent the opportunity cost associated with investing money in the enterprise (Workman 1986).

Table 2. Annual cash flow parameters for a stocker cattle enterprise on a shallow prairie range site.

	With prescribed burning				Without prescribed burning			
	Risk			No-Risk	Risk			No-Risk
Year	Mean	S.D.	C.V.	Mean	Mean	S.D.	C.V.	Mean
1	4224	10018	2.37	4426	5970	17313	2.90	7369
2	6565	11816	1.80	6879	5639	16662	2.95	6634
3	7914	13670	1.72	8627	4838	16594	3.43	5974
4	8543	13440	1.57	8923	3673	13828	3.76	5372
5	8609	13741	1.60	9190	4454	13732	3.08	4787
6	9362	13589	1.45	9371	3708	12215	3.29	4111
7	9568	13832	1.44	9583	3090	1955	3.54	3513
8	9578	13964	1.46	9830	1662	11284	6.78	2924
9	10958	13121	1.20	11118	1014	9263	9.13	2448
10	12036	13822	1.15	12450	−134	4175	31.15	1890
ACF[1]	87,357			90,397	33,914			45,022
NPV[2]	71,075			71,559	29,170			38,108

[1] Accumulated cash flow
[2] Net present value (4% discount rate)

Table 3. Annual cash flow parameters for a stocker cattle enterprise on an eroded prairie range site.

	With prescribed burning				Without prescribed burning			
	Risk			No-Risk	Risk			No-Risk
Year	Mean	S.D.	C.V.	Mean	Mean	S.D.	C.V.	Mean
1	−2784	3414	1.23	−2769	2273	12320	5.42	2754
2	−665	4875	7.33	−464	1835	10684	5.82	2489
3	985	6948	7.05	1340	704	9657	13.72	1664
4	1100	6995	6.35	1691	825	9700	11.76	1515
5	1172	6837	5.83	2016	899	9846	10.95	1324
6	666	7369	11.06	2256	−210	9648	45.94	1100
7	711	6831	9.61	2529	−196	8469	43.21	1003
8	1392	6339	4.55	2840	−1840	9428	5.12	−391
9	481	7514	15.62	3193	−3168	8226	2.60	−1836
10	685	7128	10.40	3592	−3873	8221	2.12	−2801
ACF[1]	3,743			16,224	−2,751			6,821
NPV[2]	2,372			11,652	−549			6,975

[1] Accumulated cash flow
[2] Net present value (4% discount rate)

and higher annual returns on burned ranges in the final 7 years of the planning horizon. Accumulated cash flows under prescribed burning greatly exceed no-burn cash flows in both the stochastic and deterministic analyses. However, because the primary income generating potential of burned range sites occurs in later years, a majority of these cash flows are heavily discounted. Therefore, the profitability of prescribed burning, as measured by the difference in burn and no-burn returns, is reduced. The difference between the NPVs derived with and without prescribed burning is $2,921 and and $4,677 under risk and no-risk conditions, respectively.

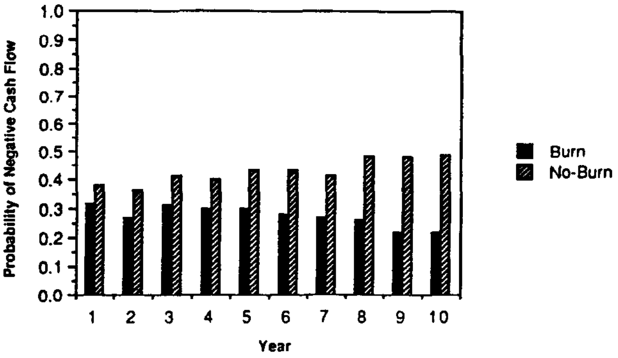

Fig. 4. *Probability of negative annual cash-flows over the 10-year time horizon, shallow prairie range site.*

Despite the short- and long-term benefits of prescribed burning, the accumulated cash flow from stocker production on eroded prairie is quite low under the economic assumptions of the analysis. Under stochastic conditions, the stocker enterprise nets less than $375 per annum when used in conjunction with prescribed burning and $275 per year without a burning program. Similarly, average annual cash flows from the deterministic analysis range from only $682 to $1,622.

As on shallow prairie range sites, the adoption of prescribed burning decreases the risk inherent in the summer stocker enterprise. When measured by the variance and coefficient of variation of annual cash flows, the variability of annual returns is greater under no-burn conditions. Also, the probability of negative annual cash flows from the no-burn scenario exceeds that derived from the prescribed burning scenario in all but the first 2 years of the 10-year planning horizon (Fig. 5).

Summary and Conclusions

Stochastic simulation and deterministic results indicate that prescribed burning is an economically feasible range improvement practice for eastern redcedar control on both shallow prairie and eroded prairie range sites. Under deterministic conditions, the NPV of returns from the burning scenario exceed those from the no-burn scenario by $33,451 on shallow prairie range sites and $4,667 on eroded prairie range sites. When the effects of stochastic production response, factor costs, and product prices are incorpo-

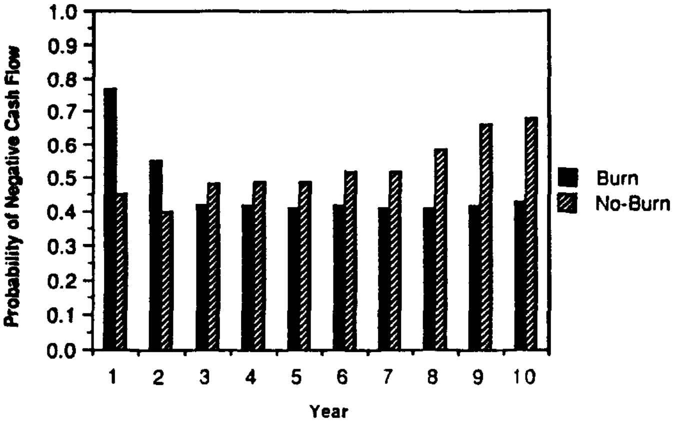

Fig. 5. *Probability of negative annual cash-flows over the 10-year time horizon, eroded prairie range site.*

rated, the profitability of prescribed burning is reduced below estimates derived under deterministic conditions. Nonetheless, NPV estimates derived from the burning scenario still exceed those estimated without burning on both range sites.

A prescribed burning program does increase the variability of annual income derived from stocker production. However, much of this increase in dispersion may be attributed to an increase in the probability and magnitude of deviations above the mean value. When risk is measured in terms of relative dispersion (coefficient of variation) and the probability of negative annual cash flows, prescribed burning is shown to reduce the risk associated with stocker production.

The results presented here should be interpreted in light of the assumptions used in the analysis. A number of factors may influence the relative profitability of range improvement investments, including weather, treatment cost, range site potential, initial range condition, and projected product and input costs. In addition, the derived results are specific to the financial, production, and resource conditions that characterize the representative ranch. Application of the model to alternative economic and environmental conditions, as well as other range improvement practices, requires respecification of the production and economic data used in the analysis.

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Book Reviews

Biochemistry of Storage Carbohydrates in Green Plants. P.M. Dey and R.A. Dixon ed. 1985. Academic Press Inc. (LONDON) LTD. 24-28 Oval Rd. London, NW1 7DX 378p. $79.00.

This book is a compilation of papers on the subject. Unlike most works that are a collection of scholarly manuscripts, *Biochemistry of Storage Carbohydrates in Green Plants* is amazingly complete. The editors were able to bring together a group of authors who gave thorough examination to the different carbohydrates. This work is not limited to the more common storage carbohydrates but also includes examination of some very esoteric photosynthates.

The international collection of authors included many easy to read tables and figures. This volume is well organized and is arranged in logical order. Each paper has a list of contents that makes for easy retrieval of information and should prove to be a great asset in using the volume as a reference. The different writing styles of the authors certainly make for interesting reading and break up the monotony seen in many academic texts.

Biochemistry of Storage Carbohydrates in Green Plants is an extremely thorough analysis of the study of storage carbohydrates. Although this is certainly not the last word on the subject, this book should prove to be a valuable reference and will certainly add to anyone's knowledge of plant physiology.—*David Hacker,* School of Forestry, Stephen F. Austin State University. Nacogdoches, Texas.

Environmental Economy. Edited by Richard Brooker and Matthew Corder. 1986. E.&F.N. SPON, London. 224 p. $40.00 (Cloth).

This book focuses on land restoration problems in the United Kingdom and current techniques used in land reclamation. Edited by Richard Brooker and Matthew Corder, the book is composed of 9 papers by various British authors with a broad base of experience in landscape restoration. The subject is addressed in an introductory or foundational manner. Specific topics addressed in the book vary, drawing upon the strengths of individual authors, but are organized in a logical manner with numerous subtitles and easily understood examples.

Early chapters focus on increasing the reader's understanding of common land reclamation problems in the United Kingdom, with particular emphasis on soil/site restoration. Topics addressed include topsoil substitutes, refuse screening, the use of polyacrilamides to achieve increased water and nutrient retention in very inhospitable substrates, various seeding techniques, the use of chemicals to retard grass growth, among others. Chapter 4, 5, and 6 stress the creation and maintenance of natural areas within or near urban areas as a part of the reclamation of derelict lands. Specific emphasis is placed on the use of plant materials, ponds, and the role of wildlife in relation to the creation of natural areas in the restoration process. The remaining chapters of the book include discussions of environmental education, the management of amenity grasslands and woodlands, and an analysis of future opportunities.

Although, limited portions of the book are not applicable to landscape restoration problems in the United States, due to direct references to zoning laws, funding sources, and other information specific to the United Kingdom, the fundamental concepts of land restoration discussed in the book are not country specific. Differences between the United States and the United Kingdom are obvious throughout the book, including the vocabulary used by the authors. Although I was frustrated during the early stages of the review process by authors' use of unfamiliar words such as conurbation, colliery, and brash, as I became familiar with the terminology I found the book very interesting and enjoyable to read—*Keith A. Blatner,* Department of Forestry and Range Management, Washington State University, Pullman.

The Role of Legumes in Conservation Tillage Systems. 1987. J.F. Power editor. Published by the Soil Conservation Society of America, 7515 N.E. Ankeny Road, Ankeny, Iowa 50021-9764, 153 pgs., 8 1/2 × 11 paper, $12 postpaid.

This publication is the proceedings of a national conference held at the University of Georgia at Athens in April 1987 with the support of USDA, ARS and SCS; Tennessee Valley Authority, The National Fertilizer Development Center; and several Southern universities.

The 67 papers, many with multiple authors, were presented under 8 principal headings. The energy shortage of the 1970's emphasized the need for less expensive sources of nitrogen for use in crop production.

1. The need for legume crops, for rotations, as fallow substitutes, for soil conservation and their place in a conservation tillage system are discussed.
2. Germ Plasm Resources are given by geographic areas including an extensive list of references. Variability in root development and the effects of soil drainage, acidity, soil temperature, interseeding and water use are discussed.
3. As a nitrogen source, alfalfa, red clover, alsike and other clovers and miscellaneous legumes are reported on principally in rotation with corn and grain sorghum. Recovery rates, tillage systems crop rotations and crop yields show that nitrogen can be effectively grown.
4. Insects and diseases may increase, diminish or change with introduction of legumes into a cropping system. Examples are given of both beneficial and injurious results.
5. Cropping procedures include various conventional and conservation tillage systems using legumes as a source of nitrogen in crop rotations with corn, wheat, barley, rye and grain sorghums.
6. Weed control is important when conservation tillage is practiced. Some legumes under certain conditions become weeds.
7. Erosion and productivity are influenced by legumes and how they are handled in rotation. More research is needed.
8. The economics of using legumes in a conservation tillage system are favorable. At least part of the nitrogen requirements can be met by legumes.

Although the irrigated cropping areas of the west were largely overlooked in this symposium it is clear that legumes can reduce dependence on commercial nitrogens. With the tremendous surplus crop acreage now and for the forseeable future, more nitrogen should be produced via legumes. This publication provides an excellent overview. The organizing committee has suggested a follow-up conference.—*John L. Schwendiman, Pullman, Washington.*

1987 Reviewers

We sincerely thank the reviewers of the past year who, by their efforts, have made a significant contribution to the journal, the Society, and the profession.

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